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DISTRIBUTION PATTERNS OF LIVING AND SUBFOSSIL PODOCOPID OSTRACODES IN THE NOSY BÉ AREA, NORTHERN MADAGASCAR

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ABSTRACT

Collections of living and subfossil podocopid ostracodes from littoral and inner sublittoral environments in the Nosy Bé area of northern Madagascar are used to examine distribution in a restricted region. Coefficients of association and a clustering technique originated for numerical taxonomy and subsequently adapted for quantitative biofacies analysis yield biofacies and biotope classifications based on both living and subfossil data. The biofacies achieved by this method do not correspond to characteristic assemblages of the different biotopes, although they do describe tendencies to joint occurrence of species. The biotope classifications derived from data on occurrences of living forms are not very meaningful because of low populations of the samples. For subfossil populations this method consistently separates grossly distinct assemblages; transitional assemblages and environments are arbitrarily and variably classified.

The replicability and specificity of living associations, as tested by repeated sampling of the same species of algae, marine grasses, corals, sponges, and other host organisms, is very low, so that these microhabitats usually cannot be distinguished consistently by their ostracode populations alone.

The subfossil populations of littoral and inner sublittoral environments are derived from living associations of local microhabitats with few introduced elements. The more numerous subfossil populations of finer offshore sublittoral sediments are derived not only from indigenous populations but from littoral and shallow-water environments also, in varying proportions not highly correlated with relative abundance in life. Several possible criteria for recognizing indigenous species in subfossil populations are investigated: proportion of intact carapaces, proportion of total subfossil population, left/right ratio of single valves. None of these serve to distinguish indigenous from nonindigenous species.

Because of the obscure relationship of subfossil populations of deeper-water sediments to living associations, paleoecological interpretation of subfossil assemblages may be accomplished most efficiently by direct comparison of subfossil distribution patterns with general ecological and physical parameters of the environment.

INTRODUCTION

SCOPE AND PURPOSE OF STUDY

A basic assumption of paleoecology is that a fossil assemblage is, at least to some degree, representative of the living associations in the area at the time when the sediment was accumulating. The fossil record of a community is necessarily a selective and distorted one. Nevertheless it is a more or less direct derivative of the living assemblage, and a central aim of the study of paleoecology is to search out the rules by which we may reconstruct from the fragmentary and distorted patterns a dynamic model of the original community structure.

This study was designed to examine the living distribution and subfossil record of a single group of animals, podocopid ostracodes, in a restricted locality in order to assess the degree and manner in which the subfossil record bears witness to the living associations from which it was derived.

PREVIOUS WORK

GENERAL STUDIES

The theoretical aspects and basic assumptions of paleoecological interpretation of fossil assemblages have been the subject of many general discussions. IMBRIE (1955) recognized seven basically different methods of biofacies analysis: (1) taxonomic analysis, (2) morphologic analysis, (3) frequency-distribution analysis, (4) abundance analysis, (5) incomplete specimen analysis, (6) compositional analysis, (7) textural analysis. JOHNSON (1960) proposed three theoretical models of possible shallow-water marine fossil assemblages resulting from burial of a life assemblage, transportation of dead remains, or some combination of these processes, and listed potentially useful criteria for determining the environmental setting and past history of a fossil assemblage.

The implementation of theoretical models for application to specific fossil assemblages is accomplished by prior evaluation of possible criteria by analysis of known situations. Investigations of Recent environments using a paleoecological approach, such as JOHNSON's (1965) analysis of pelecypod death assemblages in modern sediments of Tomales Bay, California, are necessary to clarify assumptions and refine techniques for the interpretation of fossil environments.

OSTRACODE STUDIES

Although fossil ostracodes were recognized and described from the early years of the 19th century, sustained investigation of their potential usefulness as biostratigraphic and paleoecological indicators was fostered by the revived interest in micropaleontology that resulted from the great expansion in petroleum exploration following World War I. As in the case of Foraminifera, the early attempts to describe fossil ostracode species and establish them as useful paleoecologic and biostratigraphic indicators directed attention to the inadequate state of understanding of modern forms. Not only was their ecology poorly understood, but over most of the world the mere description of local faunas had barely commenced. Thus many micropaleontologists turned to the study of living species, with the double intention of establishing a consistent and paleontologically useful scheme of classification based on carapace structures and of investigating the ecological conditions characterized by modern associations. Studies by SWAIN (1955), BENSON (1959), and CURTIS (1960) are examples of efforts to relate subfossil assemblages to the ecologically significant environmental parameters in a restricted locality. It should be noted that such studies have been considerably influenced in collecting method and philosophy by earlier and concurrent micropaleontological studies of modern Foraminifera and that they have been concerned almost exclusively with assemblages of subfossil carapaces.

The ecology of living ostracodes has not been entirely ignored by any means. From earliest times taxonomists noted observations on the occurrence, distribution, and biology of living species. Many ecologically oriented monographs of local faunas exist, of which those of G. W. MÜLLER (1894) and O. ELOFSON (1941) are classic examples. Increasingly detailed attention is being given to habitats and both internal and external morphology in modern faunal studies such as those by HARTMANN (1956, 1957, 1959) of the El Salvador region. REYS (1961, 1963, 1964) made collections of living faunules from marine algae, grasses, and sandy substrates in the Marseilles region and has attempted to evaluate "host" preferences and seasonal variations in abundance. KORNICKER (1958, 1964-*17, 18*) investigated the

general ecology and distribution of living myodocopid and podocopid ostracodes in sediments of the Great Bahama Bank and of Redfish Bay, Texas. These and similar studies concerned with the living animal have usually ignored the disposition of the carapace after death and the resultant subfossil record.

Thus two distinct lines of approach, zoological-ecological and micropaleontological-paleoecological, have been made to the study of modern marine ostracode species distributions. Rarely in the literature have the two types of analysis been applied to the same local fauna. For this reason, and because the two methods employ different assumptions, methods of collection, preparation, and taxonomic identification, comparison of results is difficult and of necessity highly subjective. In all probability this study represents the first occasion on which a local ostracode fauna has been collected, prepared, described, and analyzed for distribution patterns by both methods, making possible a further attempt at comparison and coevaluation of the results.

QUANTITATIVE BIOFACIES ANALYSIS

The current revolution in analytical techniques made possible by the advent of the high-speed digital computer has brought about a healthy renewal of interest in the use of quantitative procedures for analyzing distribution patterns. For the first time, it is possible to treat quantitatively a complex situation by truly multivariate methods, the computations for which were impossible only a few years ago. Quantitative procedures also promise greater objectivity of method and conclusions, more reproducible results, and easier comparison of the results attained by different investigators, in different areas, and by using different sampling methods. The techniques of numerical taxonomy (Sokal & Sneath, 1963) have been demonstrated to be applicable and appropriate for ecological analyses by Kaesler (1966) in a trial re-examination of microfossil populations of Todos Santos Bay, first studied by Walton (1955, Foraminifera) and Benson (1959, Ostracoda). The use of quantitative procedures, none of which are new, has made possible the evaluation of an otherwise completely unmanageable volume of data.

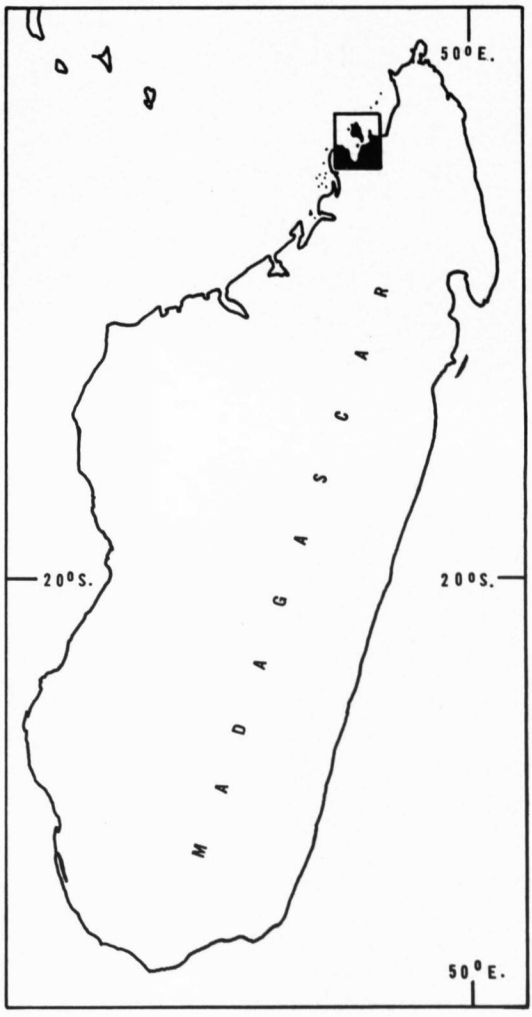


Fig. 1. Location of the study area around Nosy Bé in northern Madagascar.

DESCRIPTION OF THE STUDY AREA

GENERAL SETTING

Nosy Bé is an island roughly 14 miles long by 9.5 miles wide located six miles off the northwest coast of Madagascar (Fig. 1). The materials used in this study were collected from the shores of Nosy Bé and from adjoining waters of the Baie de Tsimipaika and Baie d'Ampasindava (Fig. 2), roughly in the area between 13°10′ and 13°40′ South Latitude and 48°10′ and 48°30′ East Longitude. An analysis by Battistini (1960) of the terrestrial and littoral geomorphology of Nosy Bé and the nearby mainland area is the principal

source of information about the geologic history of this area.

Water temperatures around Nosy Bé vary from about 24°C. in August to about 28°C. in February. The difference between lowest and highest possible tides is 4.44 m., with an average of 2.22 m. This great fluctuation in tidal level gives rise to strong tidal currents in restricted channel areas. The northwest coast of Madagascar is protected by the mainland from swell from the Indian Ocean. The waters between Nosy Bé and the mainland are generally very calm, the only sea being that produced by a diurnally changing wind that produces waves with crests usually less than one meter high. The more northern areas of the bays are open to somewhat stronger waves from the Mozambique Channel.

The waters are extremely clear except during cyclonic disturbances, when fine bottom sediments may be stirred into suspension. During the rainy summer season great volumes of extremely turbid water are discharged from the principal rivers; these water masses remain distinct and soon deposit their argillaceous burden in the depths of the bays. Water depths on the continental platform around Nosy Bé are generally shallow, rarely exceeding 40 m.

The sediments in the area are very heterogeneous; Battistini (1960) has analyzed a few of the littoral sediments, but in general the sublittoral sediments have not been described or mapped. Calcium carbonate sands, usually associated with coral masses but also with grassy expanses, are the most extensive single sediment type in shallow water (<10 m.); these are bioclastic sands composed of usually recognizable skeletal fragments of algal, coral, and other invertebrate remains in varying proportions. Sediment in mangrove areas near the mouths of small streams is soft brown sandy mud with a high content of woody fragments, derived from erosion of the lateritic clayey soil. The deltaic sediment of the Sambirano and Antsampahana rivers is well-sorted orange quartz sand. In deeper water, there are extensive areas of a gray quartz-carbonate sandy mud with variable sorting and quartz/carbonate proportions. The finest sediment, usually found at depths exceeding 15 m., is a soft gray clay, which contains a small fraction of sand-size calcium carbonate skeletal parts in an excellent state of preservation.

The warm temperatures and clarity of the waters permit hermatypic corals to flourish. Patch reefs are common in shallow areas; fringing reefs encircle the islands at the edges of wave-eroded rocky platforms. These reefs have limited vertical extent, being found on rocky platforms, and are not true reefs in the genetic sense. Battistini (1960) explains their apparent youth by the relative speed of the Flandrian transgression that submerged this region and by the minimal wave activity, which produces very little in the way of a fore-reef talus zone for outward expansion. Behind the fringing reefs dead coral fragments accumulate on the rocky platform and, with a thin cover of carbonate sand, support a luxuriant growth of marine grasses and algae, especially *Cymodocea*.

Great vertical range of tidal variation results in maximal development of the littoral zones. Each month the lowest tides expose great expanses of beach sand and rocky *Cymodocea* beds to several hours of the noonday sun; this lowest tide level represents the upward limit of growth of corals and other invertebrates that cannot withstand the increased heat, salinity, and desiccation of these occasions. Low tides greatly facilitate detailed collecting in littoral and reef habitats.

No general account of the biology of these environments exists, and many of the species of marine algae and invertebrates have not yet been identified. However the general aspect of the shore biota is similar in many respects to that described for Inhaca Island in Mozambique (MacNae & Kalk, 1958), and some species are common to both areas.

TERMINOLOGY

The terms *littoral* and *inner sublittoral* are used here in accordance with recommendations of Hedgpeth (1957). *Littoral,* "pertaining to the marginal zone of the sea" (*10,* p. 19), is here essentially synonymous with "intertidal." *Inner sublittoral* refers to the benthic environments from lowest tide level down to a depth of about 50 m., a lower limit that corresponds roughly to the lowest extent of larger algae and reef corals.

Because the definition of *fossil* is usually arbitrarily restricted to exclude remains of animals buried since the beginning of historic times, the term *subfossil* is used here to describe remains of organisms living at the present time and found in modern sediments.

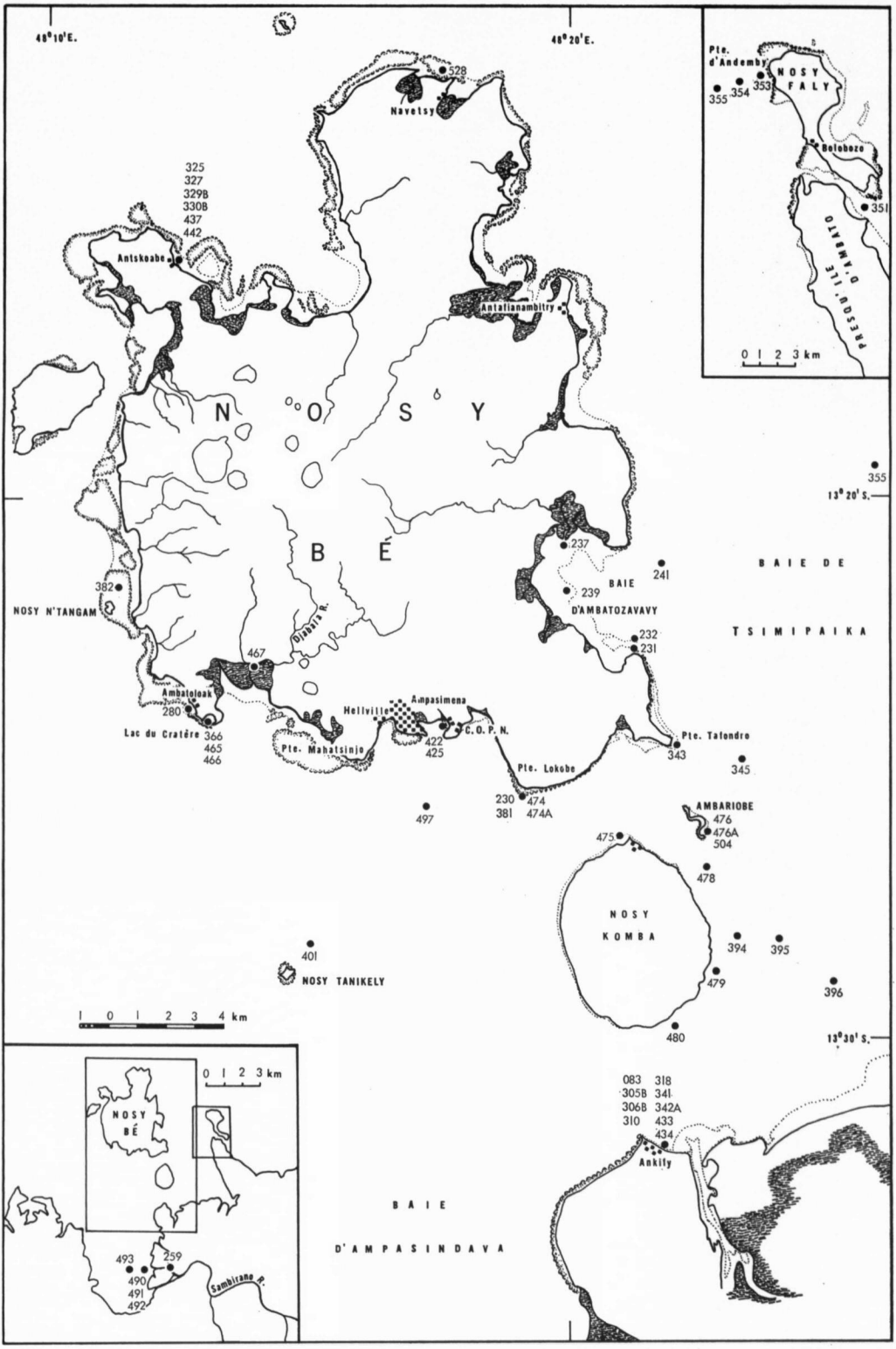


FIG. 2. Nosy Bé and neighboring mainland area, showing locations of sediment sample stations and littoral and sublittoral collecting localities.

COLLECTION LOCALITIES

The localities from which the collections for this study were made were selected on the basis of their representation of a particular type of environment, ease of access and collecting, variety of habitats, and density of population expressed within a small area. No attempt was made to sample the region completely, because of the great area involved and the relatively consistent expression of environments from place to place. Instead, a few localities were chosen as typical of each environment, and these were sampled more intensively, usually on more than one occasion. The localities sampled represent the following general types of environments: (1) coral reefs, both fringing and patch reefs; (2) nearshore wave-eroded rocky platforms with accumulations of dead coral fragments and thick stands of *Cymodocea*; (3) intertidal beach sands with beds of the marine grasses *Thallassia* and *Syringodium*; (4) mangrove-inhabited estuarine banks of small streams and nearby protected shore areas; (5) offshore sediments from depths of 2 to 30 m. The locations of the sample localities described in the following section are indicated on the map of Figure 2.

Description of Littoral and Sublittoral Collecting Localities

Loc. 1. Ambariobe.—Three small islets connected by bar of carbonate sand, shallow east side with numerous small coral patch reefs.

Loc. 2. Ambarionaomby.—Fringing reef behind which is extensive accumulation of dead coral fragments covered by encrusting organisms but without a heavy stand of grass or algae.

Loc. 3. Ambatoloaka.—Carbonate sand beach grading into coral fragment accumulations with *Cymodocea* and varied algae, fringing reef seaward.

Loc. 4. Ampasimena.—Wave-cut cliff and rocky platform covered with soft brown terrigenous mud, some mangroves.

Loc. 5. Ankify.—Broad sand beach, south side mostly quartz sand derived from Antsahampana River, north side with some calcium carbonate sand from offshore fringing reef.

Loc. 6. Antafianambitry.—Extremely broad (over 1 km.) flat sandy beach with *Thallassia* or *Cymodocea*, exposed at low tide, central part very soft black mud. A small stream empties into a broad mangrove swamp on the north edge.

Loc. 7. Bolobozo.—Rocky wave-eroded platform with covering of soft brown mud, abundant *Fucus* and *Sargassum*.

Loc. 8. Djabala River.—Mangrove-lined muddy banks of the estuary of a small permanent stream.

Loc. 9. Lac du Cratère.—A submerged volcanic crater breached by the sea with patch reefs growing around the inner margin, soft calcareous sand and mud in the center.

Loc. 10. Navetsy.—Wave-eroded rocky platform with thin covering of carbonate sand with small tide pools at low tide level and supporting many varieties of marine algae in the crevices, some coral fragments.

Loc. 11. Nosy N'Tangam.—Broad nearshore platform with dead coral fragments, thick stand of *Cymodocea*, gouged by deep barren surge channels of loose coarse carbonate sand; fringing reef seaward.

Loc. 12. Nosy Tanikely.—Well developed fringing reef on the steep north slope of this small island; patch reefs, grasses, and coral fragments on the sheltered east side.

Loc. 13. Pte. Lokobe.—Fringing coral reef around the edge of a wave-eroded rocky platform; the platform is covered with dead coral fragments and a thin layer of carbonate sand supporting a thick stand of *Cymodocea*. Fore-reef sand merges gradually with coarser and better sorted channel sands of the Passe de Nosy Vorona.

Loc. 14. Pte. Mahatsinjo.—Fringing reef around the edge of a wave-eroded rocky platform with dead coral fragments and *Cymodocea*.

Loc. 15. Sambirano River.—Mangrove-lined muddy banks of estuarine portion of major mainland river, shallow deltaic deposit of coarse yellow quartz sand at the mouth giving way abruptly to the dark clay of the Baie d'Ampasindava.

Loc. 16. Antsakoabe.—Broad carbonate sandy beach and outer sand bar, with small tide pools at low tide, few mangroves at upper level.

Loc. 17. Baie d'Ambatozavavy.—Broad marginal beach of quartz sand with *Thallassia* or *Cymodocea*, central part very soft black mud, broad mangrove swamp at the northern edge.

ACKNOWLEDGMENTS

The collections on which this study is based were made during June, July, and August of 1964 when I was privileged to participate in the U.S. Program in Biology, International Indian Ocean Expedition, supported by the National Science Foundation. Through a cooperative agreement between the U.S. Program in Biology and the Office de la Recherche Scientifique et Technique Outre-Mer, Paris, American participants in the shore collecting program at Nosy Bé were provided living quarters, laboratory space, and field assistants at the Centre d'Océanographie et des Pêches, Nosy Bé, Madagascar, of which M. Angot is Director. On several occasions dredging operations were carried out on board the small research vessel of the Centre, the *Ambariaka*, with the assistance of M. Michon, captain, and M. Pichon, zoologist, both of the Centre. The success of the collecting program is in large measure due to the efforts of Arthur G. Humes (Biology Department, Boston University), leader of the U.S. party at the Centre, who was responsible for living accommodations, collecting and laboratory facilities, transportation, customs clearance and shipping of specimens, financial transactions, and general supervision of the program. I am also indebted to Humes for suggestions on field techniques and for answering my many questions on local environments from his long familiarity with the area. I am especially appreciative of the capable assistance rendered in the field by Djaosily and Abdullah, both of the Centre.

This study of the local ostracode fauna of the Nosy Bé area forms a part of a general survey of the ostracodes of the Indian Ocean being directed by Richard H. Benson under the auspices of the International Indian Ocean Expedition and the National Science Foundation. The formal systematic description of the Nosy Bé fauna is cur-

rently (1965-1966) being undertaken by BENSON and me in conjunction with analysis of collections from other localities.

Much of the work for this report was carried out during tenure of the 1964-1965 Doctoral Fellowship in Geology of the PAN AMERICAN PETROLEUM FOUNDATION, INC., at the University of Kansas. Office and laboratory facilities were provided by the Museum of Invertebrate Paleontology of the Department of Geology, University of Kansas. The development of many of the ideas presented in this paper has been stimulated by conversations with ROGER L. KAESLER (Department of Geology, University of Kansas) to whom I am also indebted for the use of several computer programs and for a great deal of advice and encouragement in the use of the computer and the application of quantitative methods to ostracode ecology. The clustering program used was written by JOSEPH FELSENSTEIN (Zoology Department, University of Chicago). Computations were carried out on the IBM 7040 digital computer of the University of Kansas Computation Center, under a University allocation.

This report was submitted in thesis form to the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Geology, under the direction of RICHARD H. BENSON. I am indebted to RICHARD H. BENSON, to ROBERT R. SOKAL whose courses on biological applications of statistical methods provided the motivation and techniques for the statistical analyses used here, and to WILLIAM M. MERRILL for valuable criticism of the manuscript.

PROCEDURE

FIELD METHODS

A variety of collecting methods were used, the choice of method being dependent on the type of habitat, the depth of water, and the purpose for which the sample was taken. In the littoral zone, all samples were taken by hand during a period of exposure at a low spring tide level. Grasses, algae, and larger invertebrates were picked by hand and isolated in plastic sacks in sea water. Large sediment samples were taken with a hand trowel and similarly retained in plastic sacks. A few short cores were taken by hand with a two-inch diameter plastic core liner on certain of the beaches. Below low tide level to a depth of about 15 feet (*i.e.*, all collections made in the reef zone and many of those on the rocky platform-*Cymodocea* beds) plant and animal specimens were collected by hand underwater and isolated in plastic sacks with sea water. Sediment samples were gathered by hand or with a modified version of the BKB miniature pipe dredge (BENSON & KAESLER, 1965). The usual time of collection was during low tide level of a spring tide.

In making these collections care was used to eliminate visible sources of contamination, in order to sample microhabitats as precisely as possible. For example, in the collection of marine grasses the stems were broken off above the sediment level and only the upper part of the plant picked, to avoid the possibility of introducing sediment-dwelling forms with the sediment around the roots. Picking was done as gently as possible so as not to disturb the organic slime, sediment, and smaller algae that cover every surface on the sea floor and provide a habitat for many microorganisms. Each specimen of alga, grass, or invertebrate was isolated separately in a plastic sack to prevent possible mixing of faunules; the independence of these samples permits testing both for specificity of "host" and for replicability of populations in independent samples of the same "host." In the case of corals, however, after the first few samples little attempt was made to isolate specimens in separate containers, because there was not sufficient indication of specificity of "host" to justify the inconvenience of this procedure.

Many of the sediment samples included in this study were collected with a small version of a Van Veen-type grab sampler that could be lowered by hand from the rubber boat used for these operations. A weighted version of the BKB dredge was also lowered from the boat with fair success. A few sublittoral sand samples were collected by dredging from the *Ambariaka.*

In the laboratory, each specimen of grass, alga, or larger invertebrate was washed thoroughly under running sea water and the debris collected on a 149 μ mesh sieve. This residue was either picked the same day for living ostracodes or preserved in 70 percent alcohol for future examination. A small piece of host organism was preserved in alcohol for possible future identification. In the case of sediment samples a 250-ml sample of the original sediment was retained for future reference; the remainder of the sample was washed and sieved under running sea water.

Only the fraction trapped between sieves of mesh sizes 841 μ and 250 μ was retained; the remainder was discarded. This washed sand fraction was then examined wet for living ostracodes, or a portion thereof preserved in alcohol for future examination; the remainder was air-dried for picking.

METHODS OF CLASSIFICATION AND IDENTIFICATION

NOMENCLATURAL AND ALTERNATIVE METHODS

Some taxonomic basis is prerequisite for all ecological study, because the ecologist must convey some assurance that he knows what organisms he is studying and that he is able consistently to recognize and distinguish them. He must also have some system of notation by which he may record his observations of these organisms. Traditionally and ideally such a system should be the Linnean binomial system of nomenclature, using for each taxon its formal scientific name. But this usage requires that before an ecological study can be completed, or at least published, a complete formal description and classification must be made for each new, poorly known, or previously misidentified or misclassified form included in the fauna. The investigator can do this himself for an entire fauna only if the fauna is relatively small and composed only of taxa that he is competent to describe. Even with a relatively homogeneous fauna the task of description, if done according to modern standards of quality of illustration, description, and comparison with related forms, may require an excessive amount of time relative to its contribution to the overall worth of the ecological study.

A formal taxonomic treatment was planned for the fauna included in the present study, but it soon became apparent that even this relatively homogeneous fauna (podocopid ostracodes only) was far too large (72 species, most of which are previously undescribed and few of which have been adequately described by modern standards) to be described properly within a reasonable length of time. A common solution of this problem in other groups, working with genera only and ignoring specific distinctions, is rarely possible with ostracodes because of the confusion and inconsistency existing at the generic level of the present classification. At the current rate of proliferation of generic names, many of the species of the Nosy Bé fauna ultimately will belong to genera that have not yet been established. Also this procedure would reduce the number of taxa from 72 to a figure so low that meaningful comparisons, generalizations and distribution patterns could not be made; in the case of the Nosy Bé fauna very few of the consistent associations of species are congruent with generic affinities.

Many of the Nosy Bé species have been found in IIOE collections made by the *Anton Bruun* elsewhere in the Indian Ocean (Benson, personal communication). It would be preferable to take these populations and occurrences into consideration in the definition and description of these species. For these reasons the formal taxonomic treatment of this fauna has been postponed until it can be coordinated with the study of other IIOE collections.

In this study it was necessary to devise a method that would circumvent problems inherent in a formal treatment outlined above. The method chosen and described below is essentially parallel to that of formal systematic procedure except that the designations adopted have no standing within the rules of zoological nomenclature. Also, no claims are made for completeness or adequacy of distinction or description of forms with respect to faunas or species outside this area; the system is designed for internal consistency only. The procedure probably is appropriate wherever the major interest is in the distributional patterns of the forms rather than the organisms themselves. This is particularly true when procedures of numerical taxonomy are used, wherein the species become characters of the OTU's (Operational Taxonomic Units, here the stations).

DESCRIPTION OF METHODS USED

The methods of identification and classification used for the ostracode specimens in this fauna is based on the species as a working unit. Morphologic characters are used as evidence, a common procedure that in no way implies that species recognized are not "biological species" (Simpson, 1961, p. 150-151). The definition of a

species used is that of a population of individuals incorporating limited variation in morphologic characters within each species and discontinuous variation between different species, which is a usual corollary of the biological species concept. As in conventional taxonomy, a type specimen has been chosen as name-bearer. For practical reasons this specimen is usually the only one illustrated, and only a limited attempt is made to describe the nature and extent of variation present among members of a species. Each species is here designated by a uninomial arbitrary combination of two code letters preceded by the term "species," and as such has no standing under rules of the International Commission of Zoological Nomenclature. Table 5 includes a complete list of all species discussed in this report. A brief informal discussion of each species is given in the latter part of the paper.

The type specimens of taxa recognized in this study are deposited in the Museum of Invertebrate Paleontology, University of Kansas.

MORPHOLOGIC CHARACTERS USED AS CRITERIA IN RECOGNITION OF SPECIES

Two sets of characters were used for recognizing and distinguishing species, one set for living animals and the other for subfossil carapaces. This distinction arises because for living animals certain characters are readily visible that cannot be seen on subfossil carapaces, while some features that are obvious on subfossil carapaces cannot be recognized in the living condition. Neither set is more important than the other, nor do they yield different results. Frequent cross-checking of the results of the two methods of classification showed that when one set of characters indicates (for example) separation of two species, characters can be found in the other set that will also adequately distinguish between the species. An outstanding example of this is the color pattern of the living animal, which for certain species is vivid, consistent, and more quickly recognized than conventional characters of shape or ornament. On several occasions, color patterns supplied the first clue that two species had been erroneously combined; subsequent search supplied characters observable on subfossil specimens to substantiate the distinction.

For recognition of species in living animals, the most useful criteria were found to be color pattern, carapace shape, general ornament type, and for smooth forms the density of bristles or normal pore canals. Details of surface ornament are rarely distinguishable, and such internal features as hinge, muscle scar pattern, or radial pore canals usually cannot be seen at all. The appendage anatomy was examined for two purposes only, to select a male specimen for the type if available and to ascertain the familial affinity of a species as a matter of general interest. There is not yet any evidence that species exist that are differentiable only in the structure of their appendages or genitalia without correlative differences in the carapace, but even if this is the case such species would be indistinguishable as fossils, and hence such a definition would be inappropriate to the problem being studied here.

The characters used for subfossil carapaces are those used for standard micropaleontological description: carapace shape, external ornamentation, hingement, normal pore canals, radial pore canals, and muscle scar pattern, in descending order of necessity. It should be noted that for mere distinction of species within a single fauna it is not necessary to have recourse to the more difficultly observed internal characters; this fact facilitates rapid classification of large populations and also explains why the work of the earliest systematists is still useful despite the few characters observable with the poor optical equipment available to them.

MYODOCOPID OSTRACODES

Myodocopid ostracodes, belonging to the groups Cypridinacea and Cladocopina, were abundant and consistent components of nearly every living ostracode fauna sampled. At least 25 species are present in the Nosy Bé fauna, all of them benthonic and a few of them burrowing forms. A very few cypridinacean specimens were found in dry sediment samples; the preservation of appendages shows that they were living at the time of collection. No truly subfossil carapaces of myodocopid ostracodes were recognized in the populations of this study. For this reason, and because distinction and identification of most myodocopid species requires more careful exami-

nation of the soft-part morphology than for podocopid species, the Myodocopida are not included in this survey.

EXTRACTION OF DATA

ADEQUACY OF SAMPLING

A basic assumption of biofacies analysis is that "a sample adequately represents the population of organisms at a station" (KAESLER, 1960) because sampling theory provides the only method of predicting parameters of an infinite population. Every effort should be made to ensure adequacy of sampling by planning of careful and consistent sampling design, and wherever possible the sampling method itself should be tested in the course of an investigation. Nevertheless adequacy of sampling always remains an assumption and as such should be periodically re-examined. It should also be remembered that adequacy of sampling depends on the purpose for which samples are taken, and that even "inadequate" samples may yield useful information if interpreted carefully. This is frequently the case for populations of living ostracodes, for which few samples are large enough for an "adequate" sample, statistically speaking, yet limited conclusions can and must be drawn from such samples.

PRESENCE/ABSENCE RECORDS

In the analysis of species distribution patterns the basic unit of data is the observational record of occurrence of a species at a particular station. This occurrence may be recorded simply as presence or absence, as in the familiar species list; or some attempt may be made to indicate the relative or absolute abundance of the form, usually numerically. The difficulties of working with presence/absence data have long been known from efforts to compare species lists. A species list that cites mere presence underestimates the importance of the few very abundant forms and often greatly overemphasizes the importance of the rare forms.

Moreover, records of presence and absence are not equivalent, in that the logical inferences that may be drawn from these data are not parallel. A record of living presence of a species at a station requires the assumption that the species lives at that station. Records of a species at two stations suggest that the species lives at both stations and that there must be some environmental or other similarity between the stations that permits this species to live at both of them. But the absence of a record for a species at a station does not unequivocally imply that the species does not or cannot live at that station, merely that for reasons unknown the species was not recorded at the station. Lack of record for a species at two stations permits the same ambiguity: the species may in fact be absent at both stations or absent at one station and merely unrecorded at the other, or merely unrecorded at both stations.

Coupled with adequate sampling procedures, lack of record may be equated arbitrarily with true absence. Yet absence still need not be for the same reason at the two stations, and thus no direct similarity between the stations may be inferred logically on this basis alone.

Likewise the joint record of two species at one station implies that they both do indeed live there, and that there is some similarity in their needs that is fulfilled at this station; the joint absence of two species at a station may be due to the same or different causes, and no conclusion may be drawn about the similarity of the needs of the two species or about environmental conditions at the two stations.

ABUNDANCE MEASURES

In order to interpret the importance of the presence of a species more adequately, an attempt is often made to assess the abundance of the species by a number, most commonly by a count of individuals. The possible values such a measure may take on are the set of all positive integers and zero. If these data are to be treated by statistical methods that assume an underlying continuous distribution, they must be transformed by some means to compensate for the discontinuity and truncated lower limit of this distribution. The "importance" of a species is not perfectly measured even by this count of individuals observed. The only abundance measure available for the absence of a record for whatever reason is zero; the logical implications of this record are the same as those of presence/absence data: the species is present but did not happen to

be recorded, or the species is present but so rare that a numerical measure of its abundance is not significantly different than zero, or the species is truly absent but for reasons not inferable. A count of one specimen permits the same conclusion as a present record in presence/absence data, that the species does live at that station. A count of two specimens, however, does not permit twice as strong a conclusion; the logical inference remains the same as for one specimen while the abundance measure has doubled. Even a count of ten specimens, while providing additional assurance against the probability of error, permits only the same logical conclusion as the count of one specimen, while the abundance measurement is ten times as great. The mathematical relations, as well, are discrepant: the consequences of a difference of one specimen may be a profound difference, as in the difference between records of zero and one, or a very significant difference, as in the difference between records of one and two, or a negligible difference, as in the difference between records of 100 and 101. Transformation of counts to some other scale, particularly a logarithmic or square root scale, may help to minimize these difficulties, except for the difference between zero and one.

BASE FOR COMPARISON OF COUNTS

In order to permit meaningful comparison of counts, there must be some uniform basis on which the counts are made. This base may be areal, as in the number of individuals per square meter, or volumetric, or based on wet or dry weight, or even based on the population itself, as proportion of the total number of organisms observed. The base must be selected independently for each type of organism and distribution problem being studied, and it must be selected before collecting, as it is one of the major factors controlling choice of sampling technique.

The bases commonly employed for comparison of subfossil ostracode assemblage counts are generally similar to those used in the study of Foraminifera. In a common sampling method, based on known area and volume, a sediment core of known daimeter, usually about 1.5 inches, is taken and the surface portion, measured usually to a depth of 1 cm., is picked in entirety for foraminiferal specimens. This method provides a precise estimate of the absolute abundance of a species areally. A major defect, however, is that the total number of subfossil specimens recovered from the sample is a function not so much of the absolute abundance of Foraminifera in the area as of the rate of sedimentation; sediments of different types yield grossly unequal total populations. Thus comparison of total population or absolute species counts can be made only for sediments of similar type and environmental origin except where additional information is available on the rate of sediment supply. Otherwise species counts must again be reduced to some common basis for comparison, usually to proportion of total population count. The volume of sediment collected by the technique described above generally yields rather high population counts of Foraminifera but very much smaller populations of ostracodes, by a factor of 10 or so, so that reliable estimates of proportions of total parametric population represented by a species cannot be made from so small a sample. For these reasons there has been much interest in using a base for counting based directly on proportion of total sample population. Such a method can bypass the complicating factors of absolute population abundance and rate of sedimentation to concentrate on the relative relationships among species; it is also not dependent on quantitative sampling and can be applied to samples taken by many different methods.

The total number of specimens that should be collected from a population in order to estimate species proportions with a given reliability can be calculated by statistical sampling theory if some assumption is made about the frequency distribution involved and randomness of sampling. For microfaunas a figure of 300 specimens has been recommended as an optimal value to combine reliability of estimate of proportions with economy of labor. This figure was derived for heavy mineral counts by Dryden (1931) and has been used successfully for foraminiferal assemblages (Phleger, 1960). Certainly for homogeneous sediment samples in which the organisms can be considered to behave like the other sand grains, this technique will be reliable. For ostracodes it is doubtful whether either homogeneity of sample or uniformity of behavior can be assumed for most samples. Species of ostracodes differ in specific

gravity and shape, more so than Foraminifera, and present the additional complication of occurring in either of two phases, as whole carapaces or single valves. Thus shaking or other disturbance may cause differential settling of specimens and resultant dishomogenization of the sample. It is a matter of general observation that when a vial of sand is shaken gently the calcium carbonate and inorganic components will separate, the skeletal fragments rising to the top because of their lesser density and more irregular shape. This phenomenon, if it affected all species equally, would be a convenient method of concentration; but it probably affects dissimilar species differently. Certainly the radically different shape and specific gravity of whole carapaces and single valves must cause them to be segregated somewhat under these conditions. Thus the relative proportions of species will be doubly distorted, by shape-dependent differential sorting and by selection for differing carapace/valve ratios among species.

A preliminary analysis of this problem was made at the beginning of the study with the intention of testing the usefulness of the 300-count method of sampling a population. Each of the subfossil populations of this study is based on a random homogeneous sample of one dram volume taken from the dried 250-841 μ fraction with the aid of a sample splitter. This vial was stored without shaking or other appreciable disturbance and picked in the conventional manner by shaking sand grains off the top onto a flat picking tray. The first 300 specimens picked were segregated and counted separately, and the remaining sample was picked completely or partially for a count or estimate of the entire fauna. Seventeen samples, representing various sediment compositions and faunal assemblages, were used for this comparison. An analysis by χ^2 of species counts based on a 300-count and on the total vial population showed no evidence that the two sets of counts came from separate statistical populations; this was true both for station and species comparisons. This analysis was performed on three types of count data: total number of specimens, number of whole carapaces only, and number of single valves only, with similar results. It may be concluded that if a careful attempt is made to maintain the homogeneity of the sediment sample, a 300-count will provide a reliable estimate of relationships in the total fauna, at least for the more abundant species. For very rare forms, this number of 300 undoubtedly is not sufficient, but the χ^2 test is not reliable for testing departures from very low expected frequencies.

For counts of living specimens of ostracodes, no useful areal or volumetric common basis for sampling and comparison has been devised. Sediment-dwelling ostracodes are so sparse in their distribution that practically no volume of sediment is sufficient to provide a large enough population for a reliable estimate of species proportions. KORNICKER (1964-*17*) said, "it is seldom that as many as 10 living ostracods are encountered in an average size core." This statement applies to a Texas lagoonal bay with maximum depth of 2 m. Deeper water sediments apparently are much less productive; the grab samples of this study of half a liter to a liter or more (though including much subsurface barren material) routinely were apparently barren or yielded less than 10 specimens after an afternoon's examination.

Ostracodes living in other habitats pose even more difficult problems. The environmentally appropriate basis for a population of alga-inhabiting ostracodes is a measure of the areal surface of the plant, which would be very difficult to estimate. Dry weight of plant or number of plant specimens can be measured but would not provide a convenient basis for comparison of assemblages among different species of plants. Corals, sponges, and other marine surfaces present similar problems of description and even greater difficulties of consistent and quantitative sampling technique.

Thus for life assemblages the only practical method of comparing counts seems to be as relative proportions of total population. Even these proportions may be less reliable than their subfossil counterparts, because most sediment samples of reasonable size yield fairly low populations of living ostracodes; however, this tendency is counterbalanced to some degree by the rather small number of species present in any one life assemblage, so that a smaller total population is adequate for reliable estimation of proportions.

Because of the difficulties of obtaining and comparing counts, increased attention is being paid to developing quantitative methods of evaluating presence/absence records. Such data must

also be taken on a uniform base for comparison; for example, an arbitrary decision must be made as to how large a sample to collect or how many specimens to pick to estimate which and how many species are present. Both total population and 300-count data are used here and yield very similar results.

CARAPACE/VALVE RELATIONSHIPS

Ostracodes present a problem not encountered in the study of other microfossils in that they may occur subfossil as either complete carapaces or as detached valves. The question of how to score a detached valve, as a single specimen or as one-half a specimen, and the additional question of if and how to count fragments of a valve have long been problematical. Certainly, insofar as the source population of living animals is concerned, a single valve is only half the remains of one animal; thus a common and logical solution scores a valve as half of a specimen. However, a count of 300 specimens for a comparison population is intended to be 300 discrete sampling units; the living-ostracode equivalent would yield an unpredictable value between 150 and 300, seriously weakening the base for comparison. The 300-counts in this study are the first 300 specimens picked regardless of whether they were double or single valves.

Another, hitherto undescribed, difficulty is presented by the different double to single valve ratios of individual species. The proportion of double to single valve specimens is by no means uniform; most subfossil faunas contain a few species that occur only as detached valves and usually one or two species that consistently occur as entire carapaces. In this respect weighting represents a less biased estimate of the source population of living animals than the simple total of discrete specimens. It also takes into consideration possible though yet unevidenced differences in double to single valve ratios among samples. An added complication: there is a slight but consistent and significant excess of left over right valves among single valve specimens in the Nosy Bé assemblages. Ideally, for accurate estimation of a living-animal equivalent, the appropriate left/right ratio for each species should be determined and applied as a corrective coefficient in estimating the number of specimens represented by single valve remains. An analysis by χ^2 showed no significant differences in left/right ratios among stations for any individual species or for total station populations, but differences among species were significant at $p < .001$, with interaction not significant. Species DD, DF, and EA display individually highly significant ($p < .001$) excesses.

FRAGMENTARY SPECIMENS

The question of if and how to rate fragmentary specimens is a recurrent one in study of subfossil populations. It is best to include at least some fragments in the counts, for certain very large or very fragile species rarely are found as intact specimens; and elimination of fragments biases the population count against these species. On the other hand, including very small fragments as individual specimens permits the possibility of counting the same animal more than once and discriminates in favor of very durable shell structures. In this study, no evidence was found of significant breakage of specimens (or separation of valves of intact carapaces, for that matter) during the washing and drying process, so that all fragmentation was assumed to date from the original history of the assemblage. The consistent policy was adopted of considering a fragment larger than one-half a valve, or so shaped that it is improbable that the complementary piece could have survived to be identifiable, to be equivalent to one valve. The great majority of such fragments are easily identifiable to species. Unidentifiable or very small fragments were ignored.

LIVING/DEAD CRITERIA

In picking and counting living populations the most difficult decision is determining that a specimen is actually living. The only sure method of making certain that a specimen is living is to observe it in motion. To observe this it is necessary to examine the sample wet in sea water as soon as possible after collection, generally within 24 hours for most species unless care is taken to maintain favorable temperature, salinity, and oxygen conditions. Sediment samples must be washed and sieved prior to examination to permit adequate visibility; thus most sediment-dwelling ostracode species can never be observed naturally

in the substrate they prefer. Algae, sponges, and other organic surfaces must be washed immediately after collection, before decomposition of the living substrate and of other microorganisms sets in. Under unfavorable conditions, some hours or days before eventual death, an ostracode will remain immobile within a closed carapace. Such specimens may be recognizable as living by color pattern or opacity of a normally clear carapace; others look essentially like entire subfossil carapaces. If the animal cannot be persuaded by taps on the carapace to show signs of movement, it may be necessary to crush the shell to be absolutely sure that the animal is in residence. Fortunately such stubborn cases are rare; most living or very recently dead specimens can be recognized easily by their characteristic color pattern.

The presence of chitinous remains of appendages within the carapace, even if fairly complete, is not a reliable indication that the specimen was living when collected. The distal parts of the appendages and heavily chitinized male genitalia may resist decomposition and persist long after disintegration of the true soft parts. It is quite usual to see molted carapaces, containing a complete internal series of appendage remains and bearing numerous exterior bristles, in the low-density sedimentary debris trapped by many algae. Such specimens can be distinguished easily from living forms by their complete transparency, caused by the absence of epidermis and true soft parts.

Animals that were living when they were dropped into alcohol, as when a sample is preserved for picking at a later date, usually open their valves and protrude their bodies, dying almost instantly in this position. Colors are much weaker but sometimes still recognizable in preserved specimens, but at any rate these can usually be identified by the yellowish opacity that is the body inside, as contrasted to the transparency of an empty smooth-shelled form.

Recognition of formerly living forms in a dried sediment sample is possible but less common, if only because living animals are so sparse in most sediment samples that the finding of one during examination of a small volume is a relatively improbable event. Such specimens usually display slightly gaping valves and sometimes have much of the body extruding. The entire body should be recognizably present though dried; vestigial remains of the most heavily chitinized parts only are not reliable indicators of a living animal. The rose bengal staining method for differentiating living from dead foraminiferal tests (Walton, 1952) cannot be used effectively with ostracodes because of the tendency of rose bengal to stain chitinous substances as well as protoplasm (Benson, 1959).

ANALYSES OF SIMILARITY

ASSUMPTIONS

The methods of biofacies and biotope analysis used here were originated for numerical taxonomy and subsequently modified for and demonstrated to be applicable to ecological analysis by Kaesler (1966). A *biofacies* is "an assemblage of . . . organisms repeatedly found together, typical of certain kinds of environmental conditions; may comprise single species or group of species belonging to one or more phyla" (Benson, 1959, p. 37). The interrelationships presumably existing among members of the biofacies and with the physical environment need not be specified or understood; thus the description of a biofacies may be in practice a faunal list. A *biotope* is "an area of which the principal habitat conditions and the living forms which are adapted to them are uniform (Hesse, Allee & Schmidt, 1937, p. 135). Adapting this concept for usefulness in quantitative paleoecological analysis, Kaesler (1966) assumed a basic premise of paleoecology, that organic remains knowledgeably interpreted are of themselves sufficient and reliable indicators or predictors of environmental conditions, and defined a *biotope* as "an area of uniform environmental conditions as evidenced by a particular fauna found in the area and adapted to the environmental conditions of the area." The environmental conditions are not known directly but implied from the inhabiting organisms; the definition of a biotope then reduces to an aggregate of localities (stations) having similar faunal assemblages.

Additional assumptions listed by Kaesler apply to the present study except as modified below:

1) "Biofacies and biotopes exist in the study area."
2) "A sample adequately represents the population of

organisms at a station." This assumption does not imply correlation between living and subfossil populations. Where evidence exists that sampling is inadequate, as in the case of the living population counts of the present study, and better estimates are not available, only tentative conclusions may be drawn.

3) "Biotopes are mappable." The term biotope is reserved here for a potentially geographically continuous unit, in accordance with KAESLER's definition, although practically speaking the sampling localities are not dispersed uniformly enough to permit making an areal distribution map. Discontinuous non-areal units, such as those defined by restriction of an assemblage to a particular type of living substrate, are termed microhabitats. The parallel assumption for such units is that they are delimitable by external ecological criteria.

4) "An adequate sample (in the sense of assumption 2) taken at any time of the year represents the population for the entire year." For the living populations this assumption may not be justified, but because no evidence to the contrary was observed this supposition is not investigated further. For subfossil populations it is assumed that sediment has accumulated over many years and represents a long-term average effect of all factors affecting composition of a subfossil assemblage.

5) "A high positive correlation exists between the distribution of live and dead organisms." It is this assumption that is being tested in the present study; hence no such *a priori* assumption is made here.

CHOICE OF COEFFICIENTS

Two simple coefficients of association are well adapted to analysis of presence/absence data, the simple matching coefficient and the Jaccard coefficient. These coefficients are evaluated, along with other coefficients that have been proposed, by SOKAL & SNEATH (1963, p. 125-141). The simple matching coefficient treats positive and negative matches as equally important. The Jaccard coefficient considers only positive matches and mismatches, ignoring negative matches.

The significance of negative matches is a controversial matter that must be re-evaluated in terms of the purposes of each individual problem. For biofacies determination KAESLER concluded (1966, p. 31) that negative matches must be ignored, because the information they give is not useful in establishing tendencies toward joint occurrence of species; hence the Jaccard coefficient is appropriate for clustering species. In clustering stations into biotopes he considered negative matches to be of equal importance with positive matches, so that two stations are similar to some extent just by being intolerable to the same species. This use of the simple matching coefficient is defensible in the case of large subfossil populations, where the dispersing effects of currents and other sedimentary agents permits the null hypothesis that the statistical probability of occurrence is the same for a species at any two stations and for any two species at the same station. Departures from probable frequencies of occurrence are attributed to non-random distributions. *A priori*, joint absences occur with expected frequencies complementary to those for joint occurrences; and they may be evaluated equivalently.

In the case of live populations, these assumptions are not tenable. Less reliable sampling and drastically fewer species occurring per station throw doubt on the rationality of an equiprobable assumption. For the populations contained in 55 sediment samples of the present study, a maximum of eight species coincide at any particular station. If the simple matching coefficient is used for such data an unnaturally high level of overall similarity results. Two stations with totally dissimilar faunas, each of maximal size, still are described by a similarity coefficient of $36/52 = 0.69$, the lowest possible coefficient in this problem. In such a case the information from negative matches submerges the more easily interpretable information of positive matches, resulting in a compressed and distorted summary of overall relations among the included stations. For the living populations, the results of analysis using simple matching coefficient were not interpretable ecologically and have not been included in this report.

Although the subfossil data can be analyzed adequately using the simple matching coefficient, the results using the Jaccard coefficient have been included for these data as well, to facilitate comparison with living assemblages. The dendrogram based on simple matching coefficients (Fig. 3) is presented for comparison with results obtained with the Jaccard coefficient (Fig. 4) and with results from studies by KAESLER and others.

It should be noted that the results obtained by the two coefficients are relatively congruent, much more so than the results obtained by different criteria for counting specimens or by comparing living with dead populations; thus consistency of method within the study is probably more critical than choice of coefficient. When the data matrix is rearranged by ordering stations and species in

the sequence yielded by the dendrograms based on Jaccard coefficients, the resulting configuration of counts shows greater density of clusters with fewer nonconforming points than does the simple matching coefficient order. Thus it may well be that the Jaccard coefficient corresponds more closely to common intuitive methods of comparing species lists.

The species distribution data and programs used for this study have been deposited with the Museum of Invertebrate Paleontology, University of Kansas.

CLUSTERING METHOD

The clustering method used in computing the dendrograms is the weighted pair group method with simple arithmetic averages; for a discussion of this method see SOKAL & SNEATH (1963, p. 182-191).

LIFE ASSEMBLAGES

HABITS AND HABITATS

MOBILITY

Most species recognized in this paper are crawling forms, climbing over the sediment surface or the surfaces of algae, corals, and other marine organisms. Only the pontocyprid forms, particularly species DE, possess any swimming capability. A few species were observed to be burrowing forms: species HF, HJ, LA, NA, A, TA.

The addition of a few drops of alcohol to a dish of sea water, an effective method of tranquilizing most small crustaceans, including cypridinacean ostracodes, has no discernible effect on the motor coordination or activity of podocopid species.

DEPTH

Cores taken of beach sand in the intertidal zone yielded no living specimens below the surface. Comparison of sediment samples taken by different sampling methods, despite inconsistencies, confirms the general opinion that living ostracodes are confined to the surface and first centimeter or so of sediment. One probable explanation for the scarcity and sporadic distribution of living specimens in many of the grab samples is that the Van Veen type sampler brings up much subsurface barren sediment intermingled with the surface material. Some dredge samples and most of the BKB samples gave apparently much greater faunas in absolute magnitude.

In the intertidal zone, an extremely productive area is the thin film of water, algae, and fine mud, not over 0.5 centimeter thick, that covers the surface of the exposed sand beach or mud flat at mid- and low-tide levels. Here the ostracodes may be collected successfully merely by saturating a dry absorbent cloth on the exposed wet sediment surface.

SEASONAL VARIATION AND BREEDING HABITS

Collections for this study were made during three consecutive winter months under essentially uniform climatic and water conditions. No evidence was observed to support any time-dependent variation in populations from which hypotheses about seasonal fluctuation in population density, breeding times, or migration might be made.

A great many females bearing eggs or early instars within the carapace cavity were collected of certain species. These species include species JB, LA, NA, XA, XB, XC, XE, XF.

POPULATION DENSITY

The problems involved in making quantitative measurements of ostracode population density have been discussed in a previous section. Although records have been kept of number of specimens per species occurring at each station of the study, no attempt was made to evaluate quantitatively absolute abundance of any of the living populations. Nevertheless some general comparisons of relative densities are possible. The largest populations of individuals and species were obtained from washings of dead coral fragment accumulations, which provide relatively large surface area and typically are covered by a great variety of encrusting organisms as well as sediment and organic debris. For the same reasons,

the encrusted and tunneled bases of living coral masses yield similar but smaller populations. The size of the population derived from washings of algae and marine grasses seems to be mainly a function of the surface area and shelter provided by the plant. Plants with tangled or bushy growth habit trap and hold much sediment and fine organic debris and provide a quiet home for many invertebrates, including ostracodes. Thus the highest absolute population density of the algal samples is supplied by alga type A, which is a tangled noncalcareous filamentous green alga resembling a snarled ball of hair.

Among sediment samples, intertidal mud flats

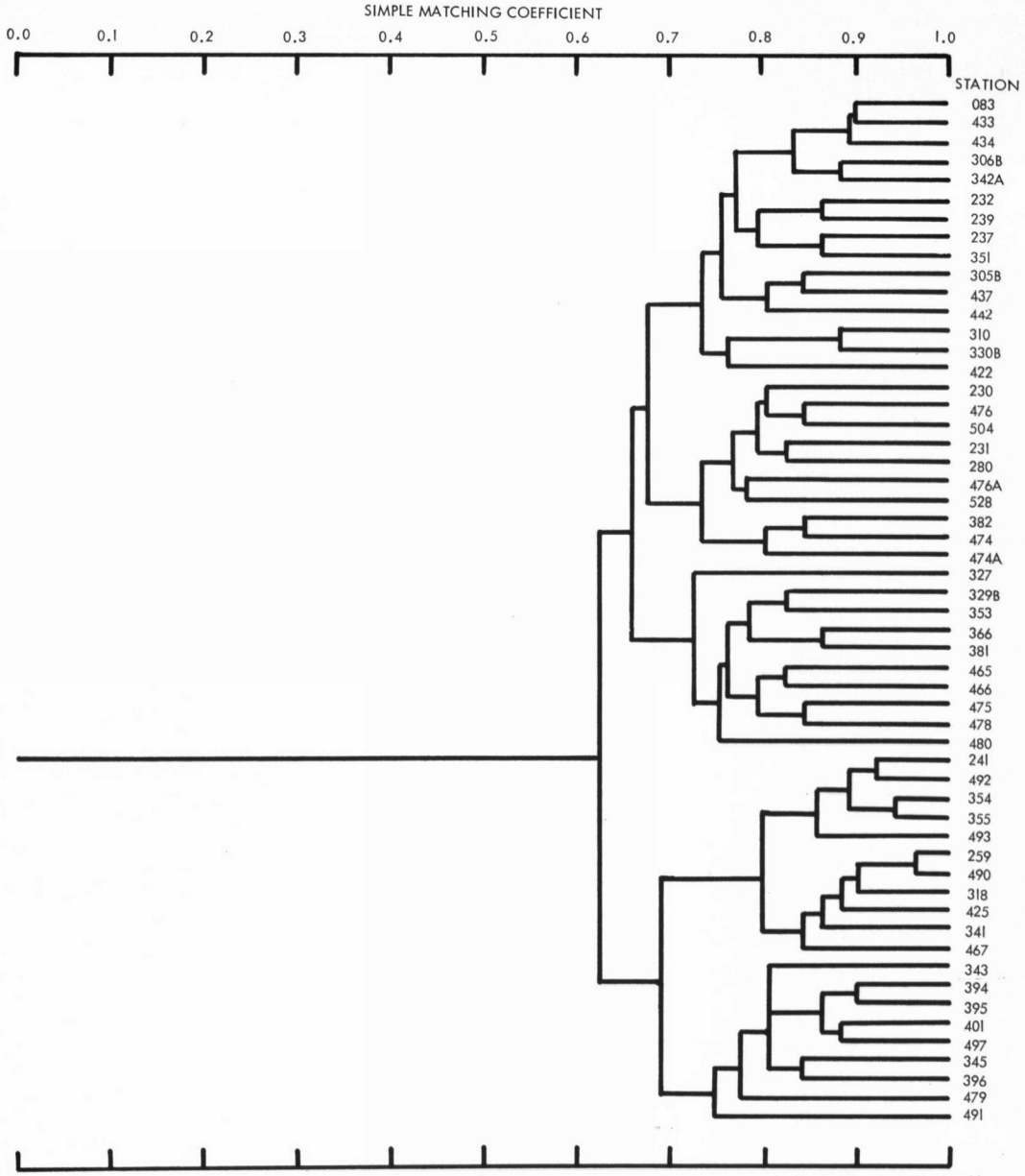


FIG. 3. Dendrogram of station similarities based on the simple matching coefficient for subfossil occurrences in the total populations of 55 sediment samples.

supply the largest populations of living ostracodes. Also productive are surface carbonate sands among living coral masses or on *Cymodocea* banks. In all these cases the high yield probably was a result of the fact that only the very surface of the sand was sampled; the high apparent faunal density probably approaches the true density, which is a function of the surface area. Sediments from deeper water taken with the Van Veen type grab sampler include an unknown but large proportion of sterile subsurface sediment; this probably accounts for the very low counts in these samples and high frequency of apparently barren samples. The modified BKB dredge does not bite as deeply and yielded some samples with larger populations.

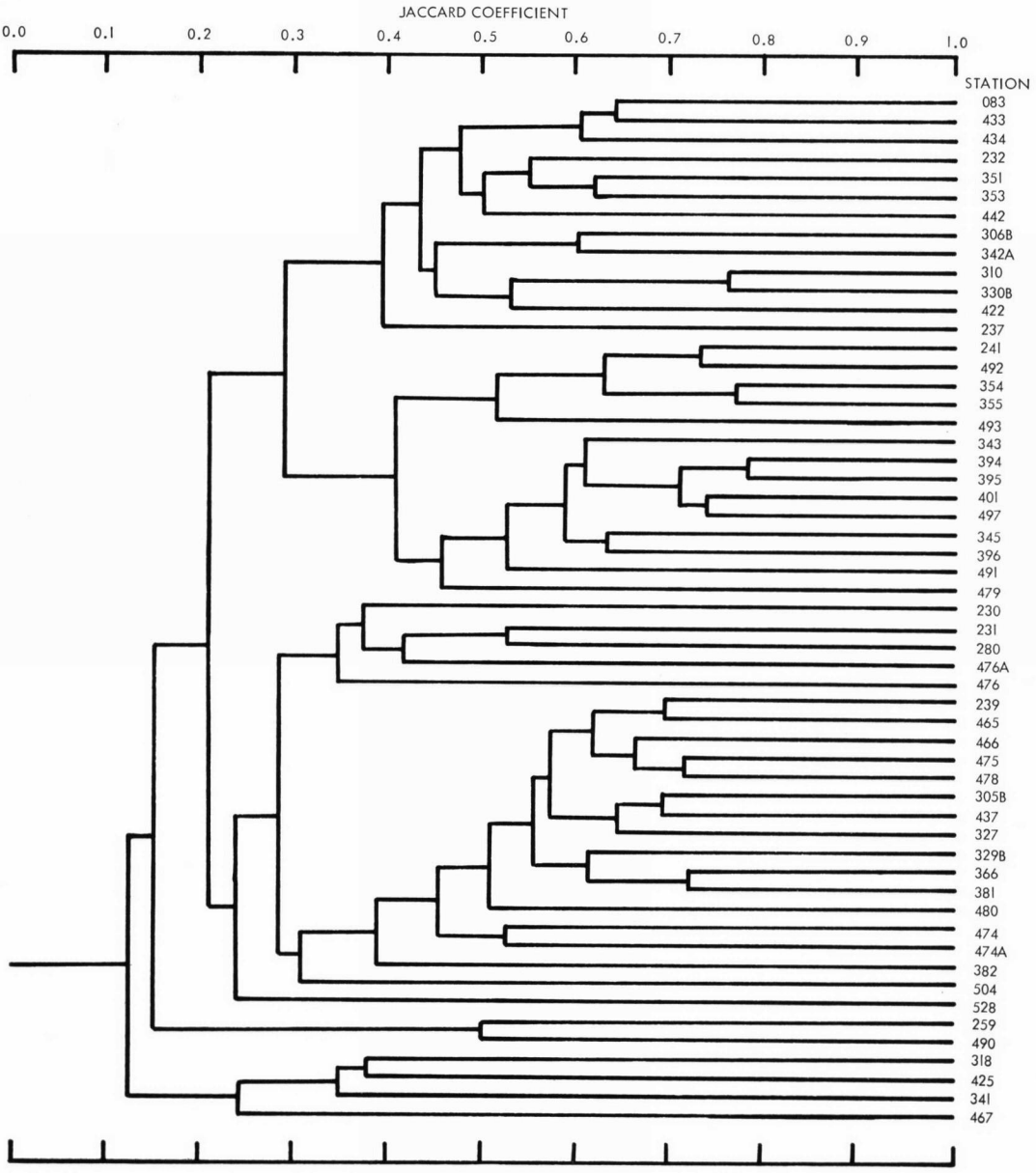


FIG. 4. Dendrogram of station similarities based on the Jaccard coefficient for subfossil occurrences in the total populations of 55 sediment samples.

MICROHABITATS

LITTORAL ZONE

SANDY BEACHES

Stranded masses of washed-in algae and sponges usually carry abundant populations of ostracodes, as do leaves of *Thallassia* and other attached grasses and small algae exposed only at lowest tides. The sand surface below mid-tide level that never dries out completely, often made more cohesive by a matting of very tiny algal filaments, has an indigenous population of crawling forms; these same forms can be found indiscriminately on larger invertebrates that trap sand, such as large starfishes, hermit crabs, and living cone shells exposed on the beach at low tide. No living

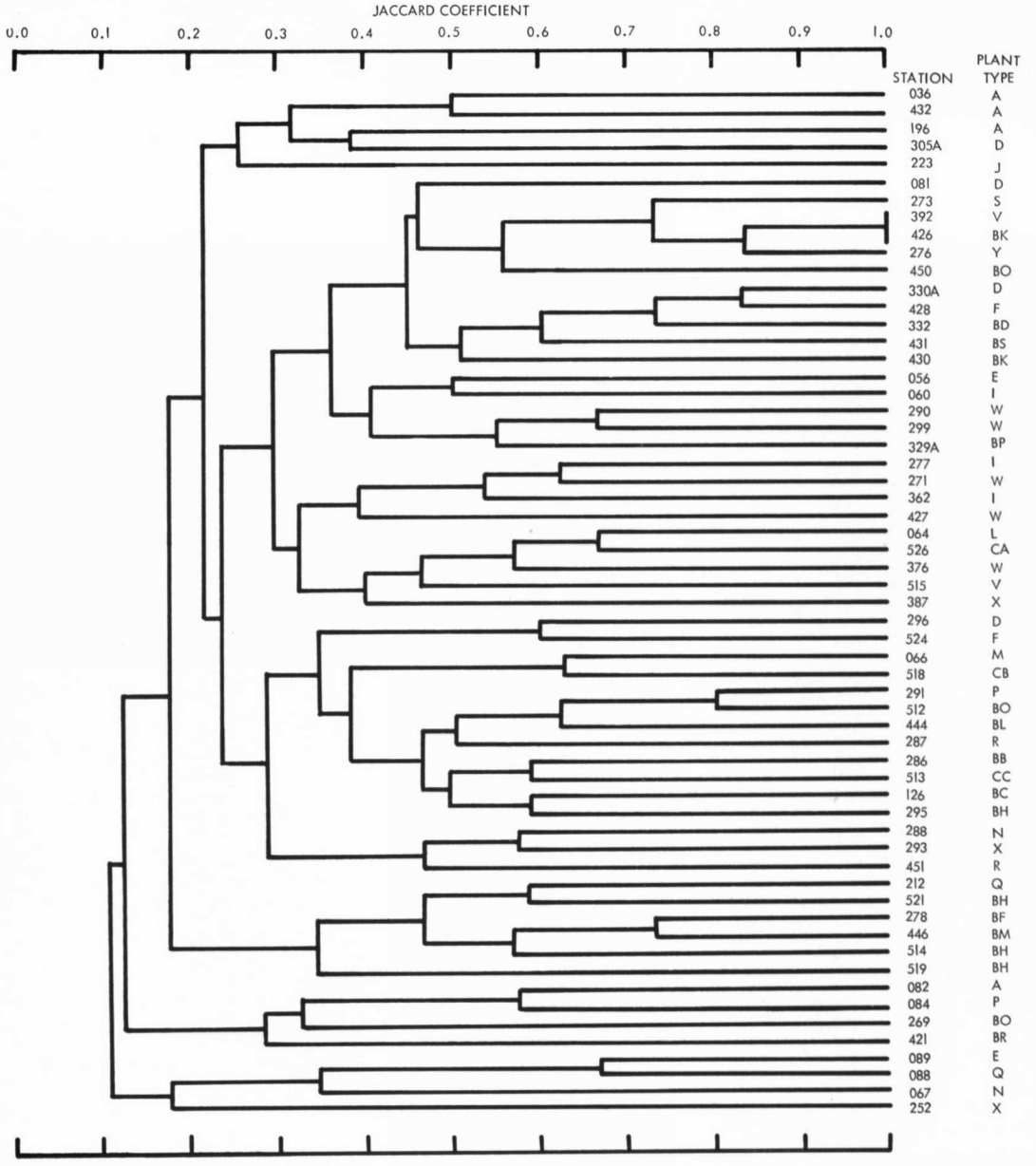


FIG. 5. Dendrogram for similarity of assemblages in living populations from 59 samples of algae and marine grasses. The letter codes designate species of living substrate.

specimens were found below a sediment depth of about one-half inch. Truly interstitial sand-dwelling forms, if present, were too small to be captured, and none were recognized.

ROCKY SHORELINE AND COBBLE BEACH

Certain green algae forming a dense mat at about mid-tide level on boulders and cliffs along the shore yield a very dense population of distinc-

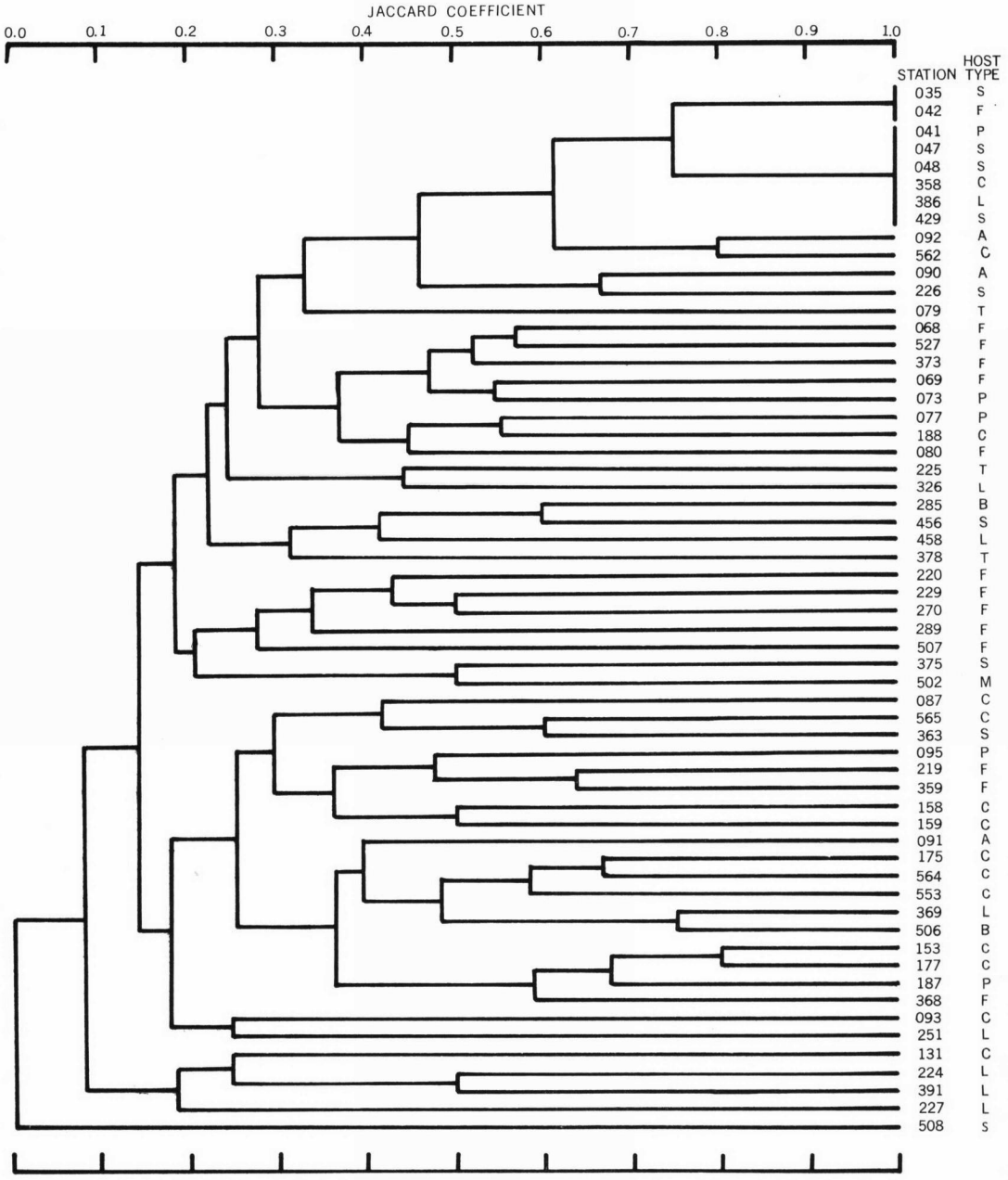


FIG. 6. Dendrogram for similarity of assemblages among 59 living populations from corals, sponges, alcyonarians, ascidians, pelecypods, dead coral fragments, and algae, based on the Jaccard coefficient. The letter codes designate type of living substrate: A—alcyonarian, B—beach sand, C—living coral, F—dead coral fragments, L—alga, M—living gastropods and hermit crabs, S—sponge, T—solitary tunicate.

tive species composition (species OC, DB, XA); these forms apparently are very tolerant of salinity differences. The covering of organic slime and fine brown mud on cobbles and the sticky surfaces of *Padina* may yield moderately abundant faunas.

MANGROVE ENVIRONMENTS

The mud- and microscopic alga-encrusted pneumatophores of the mangrove *Avicennia* on sheltered beaches near stream mouths and along estuarine channels of streams support a fauna very similar to that of the surrounding mud or muddy sand.

SUBLITTORAL ZONE

ROCKY PLATFORMS WITH CORAL FRAGMENTS AND CYMODOCEA

The broad leaves of *Cymodocea* (probably *C. ciliata*) carry a dense microflora that provides a suitable habitat for many microscopic animals including a varied assemblage of ostracodes. Their stems and the rocky or coral fragment substrate provide attachment for a great variety of calcareous and noncalcareous algae. Many of these algae are densely ramose aggregates that trap much carbonate sediment; the assemblages of these algae contain elements characteristic of the carbonate sand sediment as well as peculiarly algal forms. The large solitary red ascidian common at Pte. Lokobe is covered by a thin film of organic slime and sediment that yields similar assemblages. Rare small corals and sponges also are productive. The coral fragments with their associated encrusting organisms and covering of carbonate sand yield a very rich fauna.

CORAL REEFS

The polyp surfaces of living corals apparently

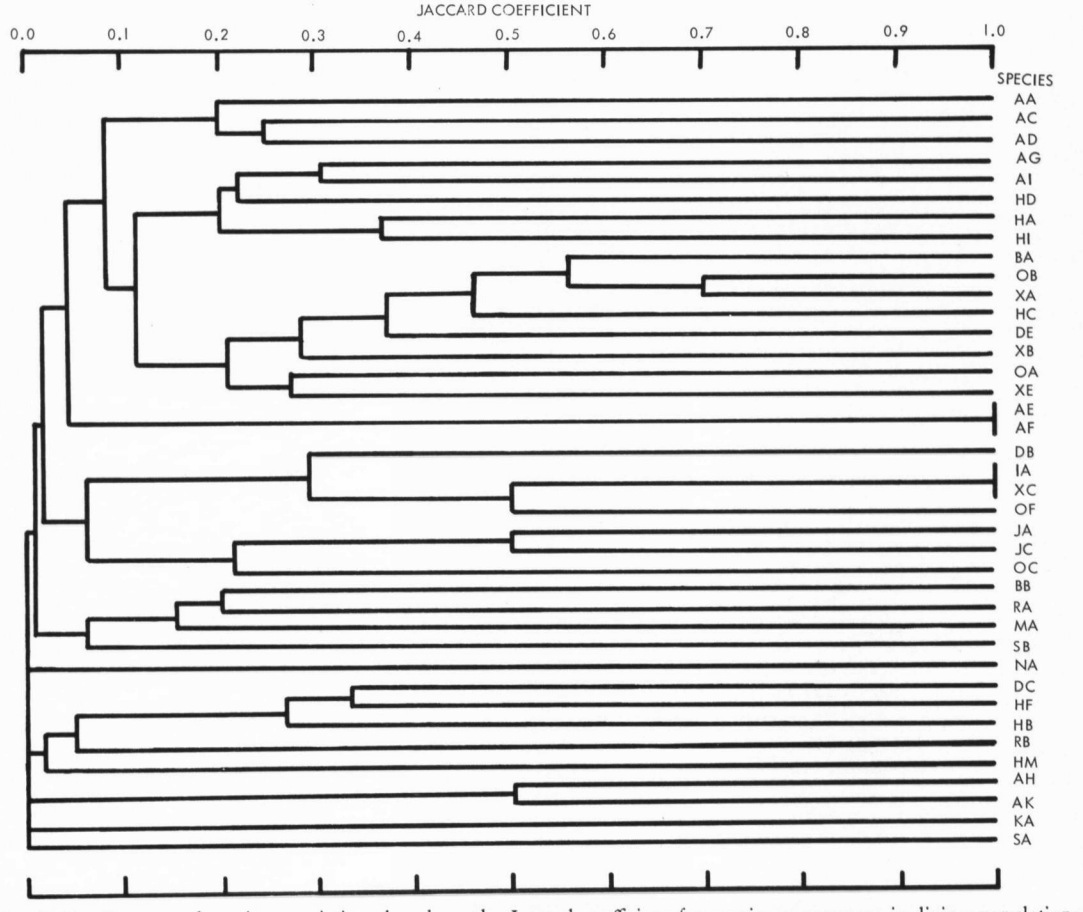


FIG. 7. Dendrogram of species associations based on the Jaccard coefficient for species occurrences in living populations from 59 specimens of algae and marine grasses.

are inhospitable to living ostracodes; the few specimens, mainly of species BA and BB, reported from this habitat may represent contamination from dead basal portions of the coral. The porous, tunneled, encrusted basal parts of the coral skeleton provide living places for many invertebrate types; ostracodes are consistently present but not especially abundant in relation to other animals.

Alcyonarians and anemones yield rare specimens of common roving species such as species BA and XA but have no peculiar fauna. They are generally quite clean of any encrusting organisms or sediment that would provide a suitable environment for scavengers.

Some sponges attract an external film of sediment that is inhabited by ostracodes, others are quite clean. No ostracodes were found living in the internal chambers, even when dense populations of annelids, copepods, and other invertebrates were present.

The exterior of the shell of the reef-dwelling giant pelecypod, *Tridacna squamosa*, is encrusted with microscopic algae and yields a typical population of roving ostracodes. Large algae are not common in the reef areas but where present have ostracode populations if growth form is suitable.

The detrital accumulations of dead coral, molluscan fragments, and coarse carbonate sand among the reef masses contain abundant populations of living forms.

OFFSHORE SEDIMENTS

Grab samples of sediments of all types from depths ranging to 40 m. yield low but characteristic populations of living ostracodes, some of which are known to be burrowing forms.

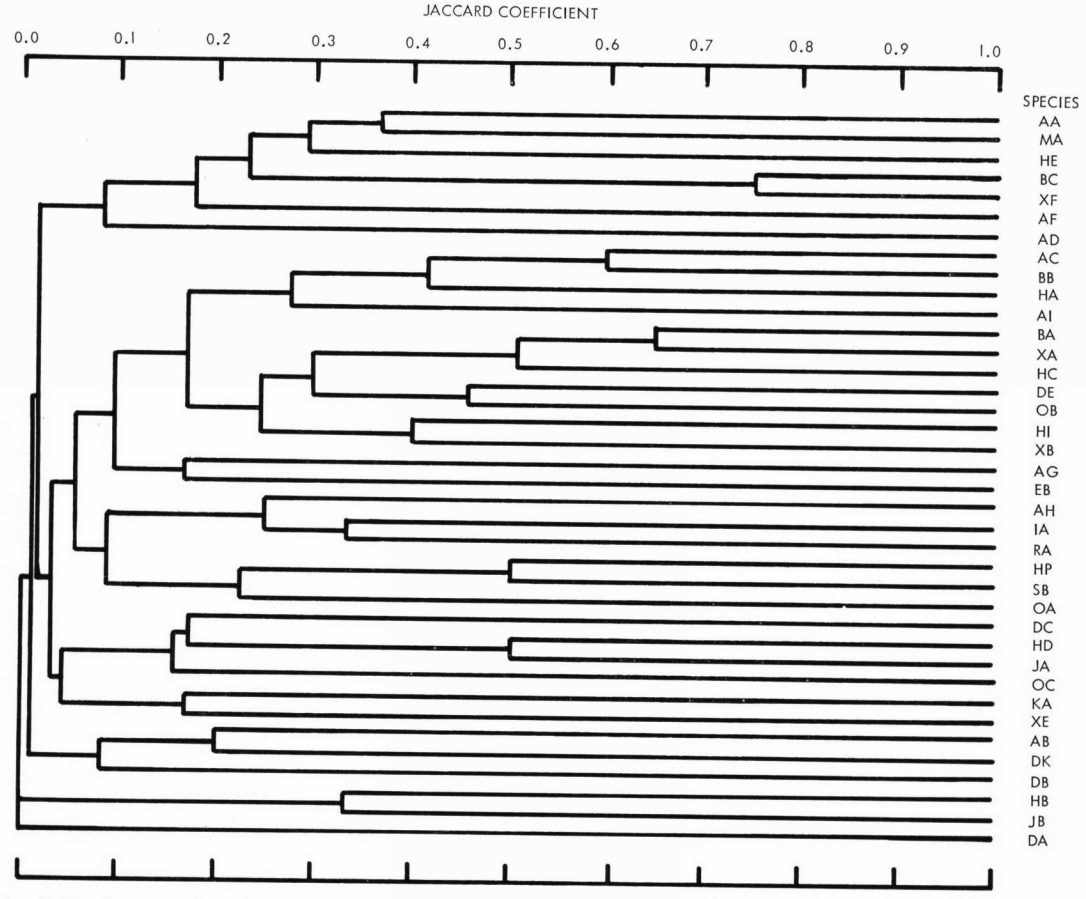


FIG. 8. Dendrogram of species associations based on the Jaccard coefficient for species occurrences in 59 live populations from living corals, sponges, alcyonarians, ascidians, pelecypods, dead coral fragments, and algae.

REPLICABILITY AND SPECIFICITY OF ASSEMBLAGES

Both in recognizing assemblages of organisms and in analyzing the distribution of these assemblages the groupings delimited are based on the recurrence and concurrence of species with greater than random frequencies. The level at which real differences can be distinguished from random differences depends on the associated variability or "error" due to sampling methods and the operation of other unrecognized factors. The variability associated with sampling living ostracode populations is innately high, for the several reasons suggested previously. In the present study it was found that repeated sampling of apparently similar microhabitats often yielded a series of conspicuously dissimilar assemblages, and that identical assemblages could be achieved by sampling from very diverse microhabitats. Partly this may be attributed to the inadequate size of many of the samples from which living populations were taken. However, these results also suggest that the classification of microhabitats for sampling purposes was done at so fine a scale as to obscure rather than reproduce the "natural" pattern, with results comparable to those obtained by using a magnifying glass to study a newsprint photo. For example, species distinctions among algae *per se* apparently have little or no effect on determining the inhabiting ostracode species; more important factors are growth habit, sedi-

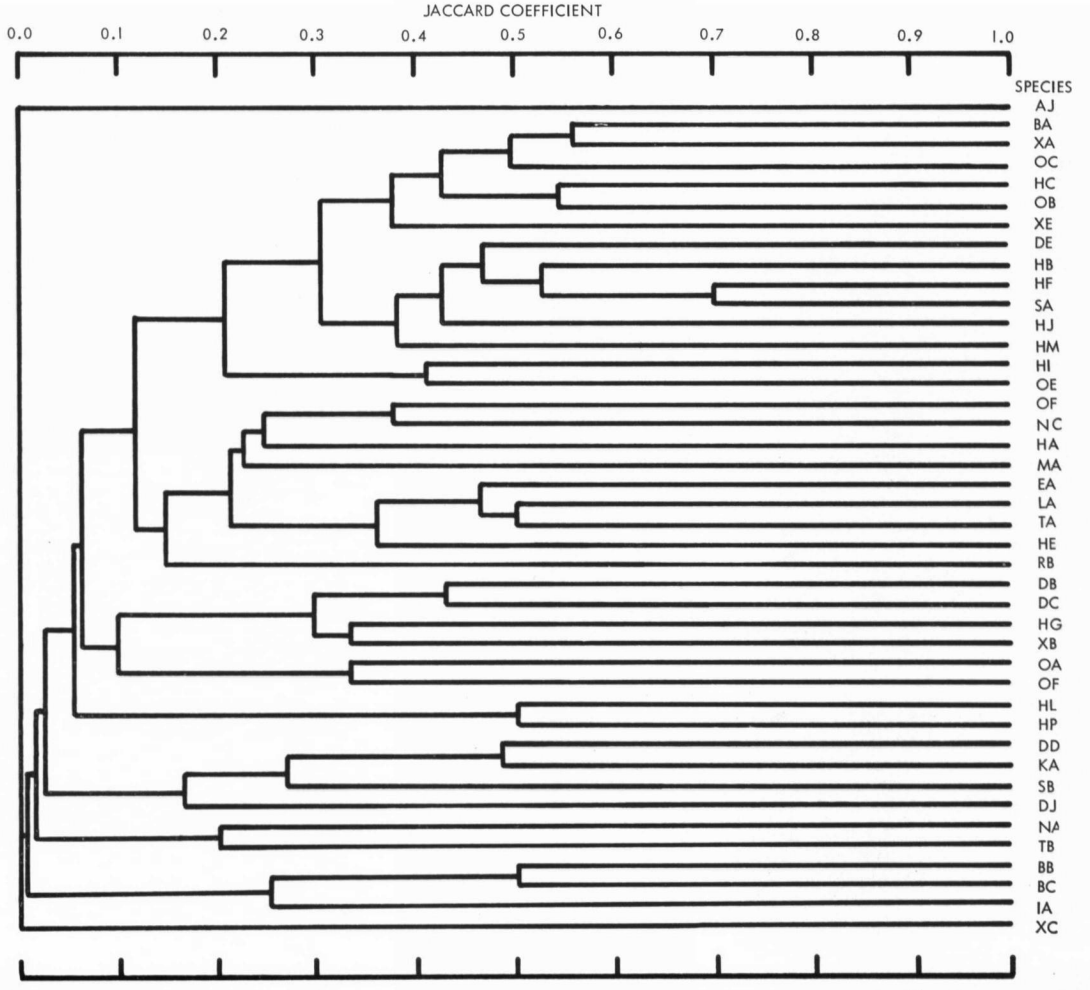


FIG. 9. Dendrogram of species associations based on the Jaccard coefficient for living occurrences in 55 sediment samples.

TABLE 1.—*Species Occurrence Records for Repeated Sampling of 19 Species of Algae and Marine Grasses.*

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES															
		BA	DB	DC	DE	HB	HC	HF	IA	OA	OB	OC	OF	RB	XA	XB	XC	XE
A	036	*	–	*	–	–	*	–	–	–	*	–	–	*	*	*	–	*
	196	*	*	–	*	–	–	–	*	*	*	*	*	–	*	*	*	–
	082	–	–	*	*	*	–	*	–	–	–	–	–	–	–	*	–	–
	432	–	–	*	–	–	–	–	–	–	*	–	–	–	–	*	–	*
	458	–	–	–	–	*	–	–	–	–	*	–	–	–	*	–	–	–

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES											
		AA	AC	AD	AE	AF	AI	BA	DE	HC	MA	OB	XA
E	056	*	–	*	*	*	–	*	*	*	–	*	*
	089	*	*	–	–	–	*	*	–	–	*	–	*

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES							
		DE	HC	HD	HI	OA	OB	XA	XE
F	057	–	*	–	–	–	–	–	–
	294	–	–	–	–	–	*	*	–
	428	*	*	–	–	*	*	*	*
	524	–	–	*	*	–	*	*	–

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES										
		AA	BA	DE	HC	HD	MA	OB	RA	SA	XA	XE
I	060	*	*	*	*	*	–	–	–	–	*	–
	277	–	*	–	*	–	*	*	*	–	*	–
	362	–	*	–	–	–	*	*	–	–	*	*
	369	–	*	–	–	–	–	*	–	–	*	–
	386	–	*	–	*	–	–	–	–	–	*	–
	387	–	*	–	*	–	–	–	–	*	*	–

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES					
		AA	AC	AD	BA	OC	XE
J	061	–	*	–	*	–	–
	223	*	–	*	*	*	*
	274	–	–	–	–	–	–

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES											
		AA	AC	AF	AG	AI	BA	BB	MA	OB	RA	XA	XB
Q	088	*	*	–	–	*	–	–	–	–	–	*	–
	212	*	*	–	*	*	*	*	*	*	*	*	*
	215	–	–	*	–	–	–	–	–	–	–	–	–
	509	–	–	–	–	–	–	–	–	–	–	–	–
	517	–	–	–	–	–	–	–	–	–	–	–	–

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES								
		AA	HA	HC	HI	OA	OB	OC	XA	XB
R	251	–	–	–	–	*	–	*	*	–
	287	–	*	–	*	*	*	–	*	*
	451	*	–	*	–	*	*	–	–	–

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES									
		BA	DE	HC	HD	JB	MA	OB	OC	XA	XB
V	224	*	*	–	–	–	–	*	–	–	–
	227	*	–	–	*	*	–	–	–	–	*
	275	*	–	–	–	–	*	–	–	–	–
	392	*	*	*	–	–	–	*	–	*	–
	515	*	–	*	–	–	–	*	*	–	–

ALGA TYPE	SAMPLE NUMBER	OSTRACODE SPECIES														
		AH	AK	BA	DE	HA	HC	MA	OA	OB	OC	RA	SB	XA	XB	XE
W	271	–	–	*	–	*	*	*	–	*	–	–	*	*	–	–
	290	–	–	*	*	–	*	–	*	*	–	*	–	*	*	*
	299	–	–	*	*	–	*	–	*	–	–	–	–	*	–	*
	376	*	*	*	–	–	*	–	–	*	–	–	–	*	–	–
	427	–	–	*	*	–	–	*	–	–	*	–	–	*	–	–

Explanation of symbols: asterisk (*) = presence, dash (-) = absence.

TABLE 1. *Continued.*

	SAMPLE NUMBER	OSTRACODE SPECIES														
ALGA		AA	AG	AI	HC	JA	JC	OA	OB	OC	XA					
TYPE	252	*	–	–	–	*	*	*	–	*	*					
X	293	–	*	*	*	–	–	*	*	–	*					
ALGA		AC	AG	AH	AI	BA	DE	HA	HC	HD	HI	MA	OB	XA	XB	XE
TYPE	295	*	–	–	*	*	*	*	–	–	*	–	*	*	–	*
BH	514	–	*	*	*	*	–	*	*	*	*	–	*	*	*	–
	519	–	–	–	–	*	–	–	–	*	*	–	–	–	*	–
	521	–	*	–	*	*	–	–	–	*	*	*	*	*	*	–
ALGA		BA	DE	HC	OB	OC	XA	XB								
TYPE	426	*	*	*	*	–	*	–								
BK	430	–	*	–	*	*	*	*								
ALGA		AI	BA	DE	HA	HC	HD	HI	OB	XA	XB					
TYPE	446	*	*	*	*	*	*	*	*	*	*					
BM	522	–	–	–	–	–	–	–	*	–	–					
ALGA		BA	DE	HA	HC	HI	HM	OB	OF	XA						
TYPE	269	–	*	–	*	*	*	–	–	*						
BO	424	–	–	–	–	–	–	–	–	–						
	450	–	*	–	*	–	–	*	*	*						
	512	*	–	*	–	–	–	*	–	*						
ALGA		BA	HI	OB	XA											
TYPE	445	–	–	*	*											
BU	525	*	*	–	–											
ALGA		AA	AG	HA	HI	OB	XA									
TYPE	510	–	–	–	*	*	–									
CB	518	*	*	*	–	*	*									
		AA	AC	AD	DB	DE	HC	HF	HI	OA	OB	XA	XB	XE		
	081	–	*	*	–	*	*	–	–	–	*	*	*	–		
Thallassia	296	*	–	–	–	–	–	–	*	–	*	*	–	–		
	305A	–	–	–	*	*	–	*	–	–	*	–	*	*		
	330A	–	–	–	–	*	–	–	–	*	*	*	–	*		
	389	–	–	–	–	–	–	–	–	–	–	–	–	–		
		AA	AC	AD	AI	BA	HA	OA	OB	XA						
	067	*	*	*	–	–	–	–	–	–						
	209	*	*	*	*	–	*	–	–	–						
Cymodocea	288	*	–	–	*	–	–	*	*	*						
	379	–	–	–	–	–	–	–	*	*						
	391	–	–	*	–	*	–	–	*	–						
	268	–	–	–	–	–	–	–	–	–						
		BA	DC	DE	HA	HM	OA	OB	XA	XB						
Syringodium	084	–	*	*	–	*	–	–	*	*						
	291	*	–	–	*	–	*	*	*	–						

Explanation of symbols: asterisk (*) = presence, dash (-) = absence.

ment trapped, and neighboring environmental conditions.

To illustrate these inconsistencies, Table 1 presents the species occurrence data for repeated sampling of several species of algae. Figure 5 shows the dendrogram of relationships based on Jaccard similarity coefficients among these and additional samples of marine plants. Table 2 presents similar data from repeated sampling of certain coral species, a sponge, and a solitary ascidian; Figure 6 shows the dendrogram computed from comparable data.

Several conclusions can be drawn from these results: 1) Because of the relative insensitivity of presence/absence data in general and the Jaccard similarity coefficient in particular, the assemblages achieved by this clustering method do not seem to reproduce any meaningful natural patterns. 2) The populations from these specimens are not large enough to be meaningfully analyzed by a statistical or other rigorously objective method. 3) The identity of the substrate plant is of minor importance in determining the inhabiting ostracode population. 4) Generalized and subjectively achieved conclusions about ostracode species distribution are nevertheless possible and should be made from such data; pooling of data or trends based on small inadequate populations, may eventually permit more penetrating and objective analyses.

TABLE 2.—*Species Occurrence Records for Repeated Sampling of Species of Corals and Other Invertebrates.*

	SAMPLE NUMBER	OSTRACODE SPECIES													
CORAL TYPE A	128	BA -													
	179	-													
	181	-													
	186	*													
CORAL TYPE B	093	AH *	BA -	XA *											
	135	-	*	-											
	156	-	*	-											
	201	-	-	-											
CORAL TYPE D	130	BA *	XA *												
	173	-	-												
CORAL TYPE F	129	BA -	HC *	XA *	XE -										
	175	*	-	*	*										
CORAL TYPE G	153	AA *	AI *	BA *	DK -	HA -	MA -	XA *							
	158	*	-	*	*	*	*	*							
	199	-	-	-	-	-	-	-							
SPONGE TYPE B	048	BA *	HC *	HE -	HI -	MA -	XA *	XB -							
	363	-	*	-	-	*	*	-							
	375	-	*	*	*	-	*	*							
SOLITARY RED ASCIDIAN	079	AI *	BA *	DE -	HC *	HD -	IA -	JA -	JB -	MA *	OB -	RA -	XA -	XB -	XE *
	225	-	*	-	*	*	-	*	*	-	-	-	*	*	-
	378	-	-	*	*	*	*	-	-	-	*	*	*	-	-

	SAMPLE NUMBER	OSTRACODE SPECIES					
CORAL TYPE J	140	BB *					
	198A	-					
	180	-					
CORAL TYPE L	177	AA *	AB *	AI *	BA *	XA *	
	182	-	-	-	*	*	
CORAL TYPE M	160	AG *	BA *				
	161	-	-				
	185	-	-				
	197	-	-				
	203	-	-				
CORAL TYPE N	172	BA *	XA *				
	176	*	-				
CORAL TYPE V	200	AD -					
	216	*					

Explanation of symbols: asterisk (*) = presence, dash (-) = absence.

QUANTITATIVE BIOFACIES AND BIOTOPES

GENERAL DISCUSSION

The use of a matrix of coefficients of association and a clustering procedure such as the weighted pair group method for defining biofacies has several disadvantages that affect the usefulness of the resulting classification. The relationship between any pair of species depends on the number of stations at which each species occurs and on what other species are included in the data, which is determined by the choice of

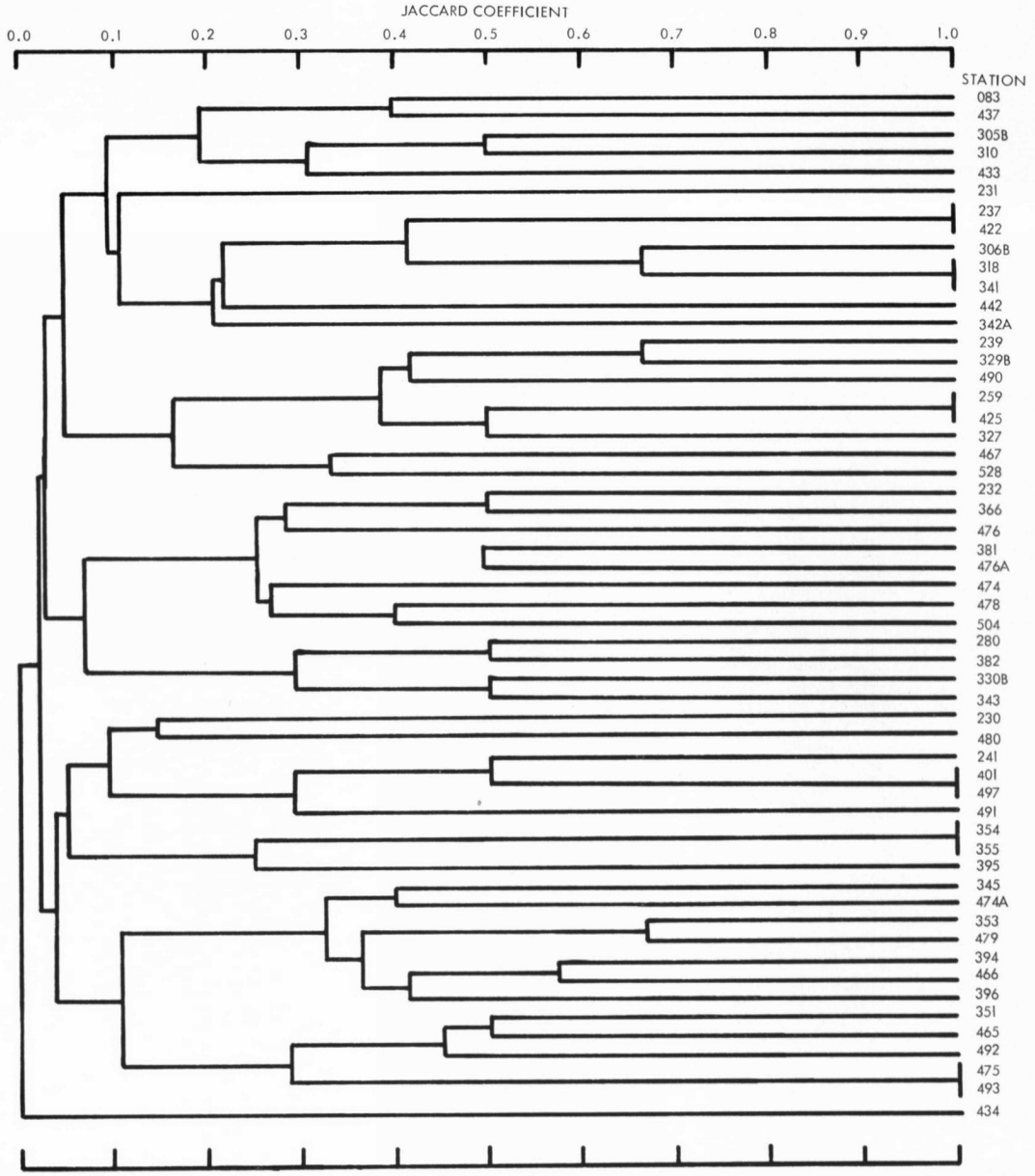


FIG. 10. Dendrogram of station similarities based on the Jaccard coefficient for living species occurrences in 55 sediment samples.

TABLE 3.—*Location, Depth, Sediment Type, Total Subfossil Population, and Biotope Classification According to the Several Methods for 55 Sediment Samples of the Nosy Bé Area.*

					Biotope Classifications at Chosen Levels of Dendrograms				
					Living		Subfossil		
					Jaccard Coeff.	S.M. Coeff.	Jaccard Coeff.		
Stat. No.	Location	Depth	Sed. Type	Total Pop.	Fig. 8	Total spec. Fig. 10	Total spec. Fig. 11	Total spec. Fig. 13	Intact spec. Fig. 15
083	Ak	I	qs	24	1	1	1	1	1
230	Lk	1	cs	29	5	2	3	–	1
231	Bz	I	cs	185	1	2	3	1	1
232	Bz	10	cs	205	3	1	1	1	3
237	Bz	I	tv	1878	1	1	1	4	3
239	Bz	5	ctv	768	2	1	4	1	1
241	Bz	12	cl	3007	5	4A	2	3	3
259	Sb	I	qv	6	2	4	6	6	2
280	At	I	cs	18	4	2	3	7	4
305B	Ak	I	qs	290	1	1	4	1	3
306B	Ak	I	qs	95	1	1	1	4	5
310	Ak	I	qcs	283	1	1	1	1	4
318	Ak	I	qs	19	1	4	7	–	5
327	As	I	cv	593	2	3	4	1	3
329B	As	I	ct	351	2	3	4	2	3
330B	As	I	cs	339	4	1	1	1	3
341	Ak	I	qs	27	1	4	7	5	3
342A	Ak	I	qs	83	1	1	1	4	5
343	Pt	2	cs	110	4	5	2	2	3
345	Pt	14	qcs	1502	7	5	2	2	3
351	Pm	1	qcs	300	7	1	1	1	3
353	Pa	10	cs	93	7	3	1	1	3
354	Pa	15	cl	13537	6	4A	2	5	3
355	Pa	17	cl	20370	6	4A	2	5	3
366	Lc	1	cs	149	3	3	4	2	4
381	Lk	2	cs	69	3	3	4	2	4
382	Nn	1	cs	23	4	2	4	8	4
394	Nk	14	qcs	1698	7	5	2	2	3
395	Nk	11	qcs	469	6	5	2	2	3
396	Nk	10	qcs	1565	7	5	2	2	3
401	He	23	qcs	677	5	5	2	2	3
422	Ap	I	tv	1274	1	1	1	1	1
425	Ap	I	tv	41	2	4	7	4	5
433	Ak	I	qcs	71	1	1	1	1	1
434	Ak	I	qcs	39	8	1	1	1	1
437	As	I	cs	296	1	1	4	1	3
442	As	I	ctv	153	1	1	1	1	3
465	Lc	5	cs	7442	7	3	4	2	3
466	Lc	5	cs	1292	7	3	4	2	3
467	Dj	I	tv	13	2	4	8	–	6
474	Lk	3	cs	66	3	2	4	8	4
474A	Lk	3	cs	94	7	2	4	8	4
475	Ay	3	cs	222	7	3	4	2	3
476	Ab	3	cs	39	3	2	3	–	4
476A	Ab	3	cs	60	3	2	3	7	4
478	Nk	10	cs	719	3	3	4	2	3
479	Nk	15	qcs	527	7	5	2	3	3
480	Nk	15	qcs	323	5	3	4	2	3
490	Ba	5	qs	10	2	4	6	6	2
491	Ba	10	cl	2234	5	5	2	3	3
492	Ba	10	cl	336	7	4A	2	3	3
493	Ba	30	cl	320	7	4A	2	3	6
497	He	20	qcs	780	5	5	2	2	3
504	Ab	2	cs	18	3	2	4	–	4
528	Nv	I	cs	40	2	2	5	–	4
Chosen level of coefficient:					0.09	0.70	0.30	0.40	0.18

Explanation of locality abbreviations:

Ab—Ambariobe
Ak—Ankify
Ap—Ampasimena
As—Antsakoabe
At—Ambatoloaka
Ay—Ambarionaomby
Ba—Baie d'Ampasindava
Bz—Baie d'Ambatozavavy
Dj—Djabala River
He—south of Hellville
Lc—Lac du Cratère
Lk—Pte. Lokobe
Nk—east and south of Nosy Komba
Nn—Nosy N'Tangam
Nt—Nosy Tanikely
Nv—Navetsy
Pa—west of Pte. d'Andemby
Pm—north of Presqu'Ile d'Ambato
Pt—east of Pte. Tafondro
Sb—Sambirano River

Explanation of depth numbers:

I—intertidal
1-30—approximate depth in meters below lowest tide level

TABLE 4.—*Biofacies Classifications Resulting from Weighted Pair-Group Method Clustering of Jaccard Coefficients from Data Representing Living and Subfossil Assemblages.*

	Living Occurrences			Subfossil Occurrences		
Ostracode Species	Algae Fig. 3	Corals Fig. 5	Sediments Fig. 7	Total Pop. Fig. 9	300 Spec. Fig. 12	Intact Spec. Fig. 14
AA	1	1				
AB		8				
AC	1	2				
AD	1	+R				
AE	4R					
AF	4R	1				
AG	2	3		1R	1R	
AH	9R	4R				
AI	2	2				
AJ				4	+R	+R
AK	9					
AL						
BA	3	2	1	6	3	1
BB	7R	2		2	4	8R
BC		1	8*	8	8R	8R
DA		+R				
DB	5	+	9	1	1	3
DC	8	6	9	3	2	3
DD			3	6	3	6
DE	3	2	2	6	3	1
DF			5	6	3	2
DG			8			
DH			9			
DJ				+	+R	6R
DK		8R		3R	2R	
EA			6	6	3	2
EB		3	2*			
HA	2	2		6	3	2
HB	8*	9*	10	6	3	1
HC	3	2	1*	6	3	1
HD	2	6				
HE		1	7	6	3	2
HF			10	2	3	3
HG			10	2	3	3
HH						
HI	2	2		2	3	1
HJ			6	6	3	1
HK				9R	4	
HL				6	3	5R
HM	+R			2	3	1
HN				4R		
HO				+R	5R	
HP		5R		9	4	5R
HQ				7	6	
IA	5R	4R		8R	8R	8R
IB				4R		
JA	6R	6R	10			
JB		9R	2			
JC	6R		10R			
KA	+*	7*	2	2	3	6
LA			7	6	3	2
MA	7	1	1	6	3	2
NA	+*		3	7	6	7
NC				6	7	2
OA	3	5	1*	2	3	4
OB	3	2	4*	6	3	1
OC	6	6	4	6	3	1
OE				6	3	1
OF	5R			3	2R	4R
RA	7	4	2*	5R	7R	
RB	+R		8R	6	3	2
RC				6	+	
RD						
SA	+*		3	6	3	1
SP	+*	5*	3	2	3	6
TA			7	6	3	2
TB				9R	5R	7R
XA	3	2	2	6	3	1
XB	3	2	2	2	3	3
XC	5*		8	5	+R	+
XE	3	7	6	6	3	1
XF		1				
Chosen level of coefficient:	0.12	0.12	0.12	0.15	0.12	0.12

Explanation of symbols:

+ Species unable to join any cluster at similarity level chosen.
R Species which is rare form occurring at only one or two stations in this group of data.
* Species more characteristic of another habitat, occurring at only one or two stations in this group of data.

stations. The clustering method used here yields mutually exclusive categories. This requirement was essential for its original application in numerical taxonomy but presents a handicap in ecological work, where overlapping associations are permissible and even desirable. According to this procedure every species must belong to a biofacies, and no species may belong to more than one biofacies. As a result, biofacies (clusters of species) resulting from the dendrograms need not correspond exactly to the faunal assemblages characteristic of the biotopes. In the data analyzed here it turns out that elements of a biofacies occur in more than one biotope, and that the characteristic assemblage of a biotope usually contains several biofacies or parts of biofacies.

For analysis of living assemblages, living population counts were classified under three headings: (1) populations from washings of marine algae and grasses; (2) populations from washings of living corals, sponges, ascidians, alcyonarians, dead coral fragments, and miscellaneous microhabitats in the reef zone and back-reef platforms; (3) living populations from sediment samples representing littoral and sublittoral environments. Fifty-five such sediment samples are included in this body of data. For these same 55 samples, the subfossil populations are analyzed by several methods: (1) species occurrences in total populations of specimens from a one-dram volume of sand fraction; (2) occurrences in the first 300 specimens picked from large faunas, total population for small faunas; (3) occurrences as intact carapaces only within the 300 specimens of method 2. Both simple matching and Jaccard coefficients were used for measuring station associations for subfossil populations. Table 3 lists the depth, sediment type, and location of each of these 55 samples and summarizes the classifications achieved by the several methods used.

(TABLE 4. *Continued*)

Explanation of sediment type abbreviations:
cl—clay
cs—carbonate sand
ct—carbonate sand with terrigenous material
ctv—carbonate sand with terrigenous and vegetal material
cv—carbonate sand with vegetal material
qcs—quartz-carbonate sand or sandy mud
qs—quartz sand
qv—quartz sand with vegetal material
tv—terrigenous mud with vegetal material

TABLE 5.—*Ostracode Species of the Nosy Bé Area with Notation of Their Occurrence as Living (L) and Subfossil (S), Page Reference to Description in This Paper, and Inferred Taxonomic Affinities.*

SPECIES	OCCURRENCE Liv.	Subf.	DESCR. PAGE	INFERRED TAXONOMIC AFFINITIES Family	(Genus)
AA	L	–	43	Paradoxostomatidae	(?Genus)
AB	L	–	44	"	"
AC	L	–	44	"	"
AD	L	–	44	"	"
AE	L	–	44	"	"
AF	L	–	45	"	"
AG	L	S	45	"	"
AH	L	–	45	"	"
AI	L	–	46	"	"
AJ	L	S	46	"	"
AK	L	–	46	"	"
AL	L	–	47	"	"
BA	L	S	47	Bairdiidae	*(Bairdia)*
BB	L	S	48	"	*(Triebelina)*
BC	L	S	47	"	*(Bairdia)*
DA	L	–	48	Pontocyprididae	*(Pontocypria)*
DB	L	S	50	Paracyprididae	*(Aglaiocypris)*
DC	L	S	49	Pontocyprididae	*(Propontocypris)*
DD	L	S	51	Paracyprididae	*(Aglaiella)*
DE	L	S	50	Pontocyprididae	*(Propontocypris)*
DF	L	S	52	Paracyprididae	(?Genus)
DG	L	–	54	Cytherideidae	(?Genus)
DH	L	–	52	Paracyprididae	(?Genus)
DJ	–	S	51	"	*(Paracypris)*
DK	L	S	51	"	(?Genus)
EA	L	S	53	Cytherideidae	*(Parakrithella)*
EB	L	–	53	"	"
HA	L	S	57	Hemicytheridae	(?Genus)
HB	L	S	60	Trachyleberididae	(?Genus)
HC	L	S	56	Hemicytheridae	(?Genus)
HD	L	S	54	"	*(Caudites)*
HE	L	S	56	"	(?Genus)
HF	L	S	60	Trachyleberididae	(?Genus)
HG	L	S	61	"	"
HH	L	–	55	Hemicytheridae	*(Caudites)*
HI	L	S	57	"	(?Genus)
HJ	L	S	61	Trachyleberididae	(?Genus)
HK	–	S	58	Hemicytheridae[1]	(?Genus)
HL	–	S	58	"	"
HM	L	S	58	"	"
HN	–	S	59	"	"
HO	–	S	59	"	"
HP	L	S	55	Hemicytheridae	(?Genus)
HQ	–	S	58	Hemicytheridae[1]	(?Genus)
IA	L	S	62	Bythocytheridae	*(Pseudocythere)*
IB	–	S	62	"	(?Genus)
JA	L	–	63	Leptocytheridae	*(Callistocythere)*
JB	L	–	63	"	*(Leptocythere)*
JC	L	–	71	?Family	(?Genus)
KA	L	S	57	Hemicytheridae	(?Genus)
LA	L	S	64	Cytherellidae	*(Cytherella)*
MA	L	S	64	Macrocyprididae	*(Macrocyprina)*
NA	L	S	54	Cytherideidae	(?Genus)
NC	–	S	54	"	"
OA	L	S	65	Loxoconchidae	*(Loxoconchella)*
OB	L	S	65	"	*(Loxocorniculum)*
OC	L	S	65	"	*(Loxoconcha)*
OE	–	S	66	"	"
OF	L	S	66	"	"
RA	L	S	66	Cytheruridae	*(Paracytheridea)*
RB	L	S	62	Bythocytheridae	*(Bythocythere)*
RC	–	S	67	Cytheruridae	(?Genus)
RD	–	S	62	Bythocytheridae	*(Monoceratina)*
SA	L	S	67	Schizocytheridae	*(Sulcostocythere)*
SB	L	S	68	"	"
TA	L	S	60	Trachyleberididae	(?Genus)
TB	–	S	60	Hemicytheridae[1]	(?Genus)
XA	L	S	68	Xestoleberididae	*(Xestoleberis)*
XB	L	S	69	"	"
XC	L	S	70	"	"
XE	L	S	70	"	"
XF	L	–	70	"	"

[1] Or Trachyleberididae.

ANALYSES OF LIFE ASSEMBLAGES

ALGAL ASSEMBLAGES

A dendrogram for species associations based on the Jaccard coefficient for occurrences in living populations from 59 specimens of algae and marine grasses is given in Figure 7. For this, as for succeeding dendrograms of species associations, the biofacies classification derivable from the diagram, usually at the 0.12 level of similarity, is summarized in a column of Table 4.

Figure 8 shows a dendrogram for species asso- assemblages from algae and marine grasses using the Jaccard coefficient. Some of these data are given in Table 1. For the most part species of algae or marine grasses cannot be distinguished consistently on the basis of the ostracode faunas taken from them.

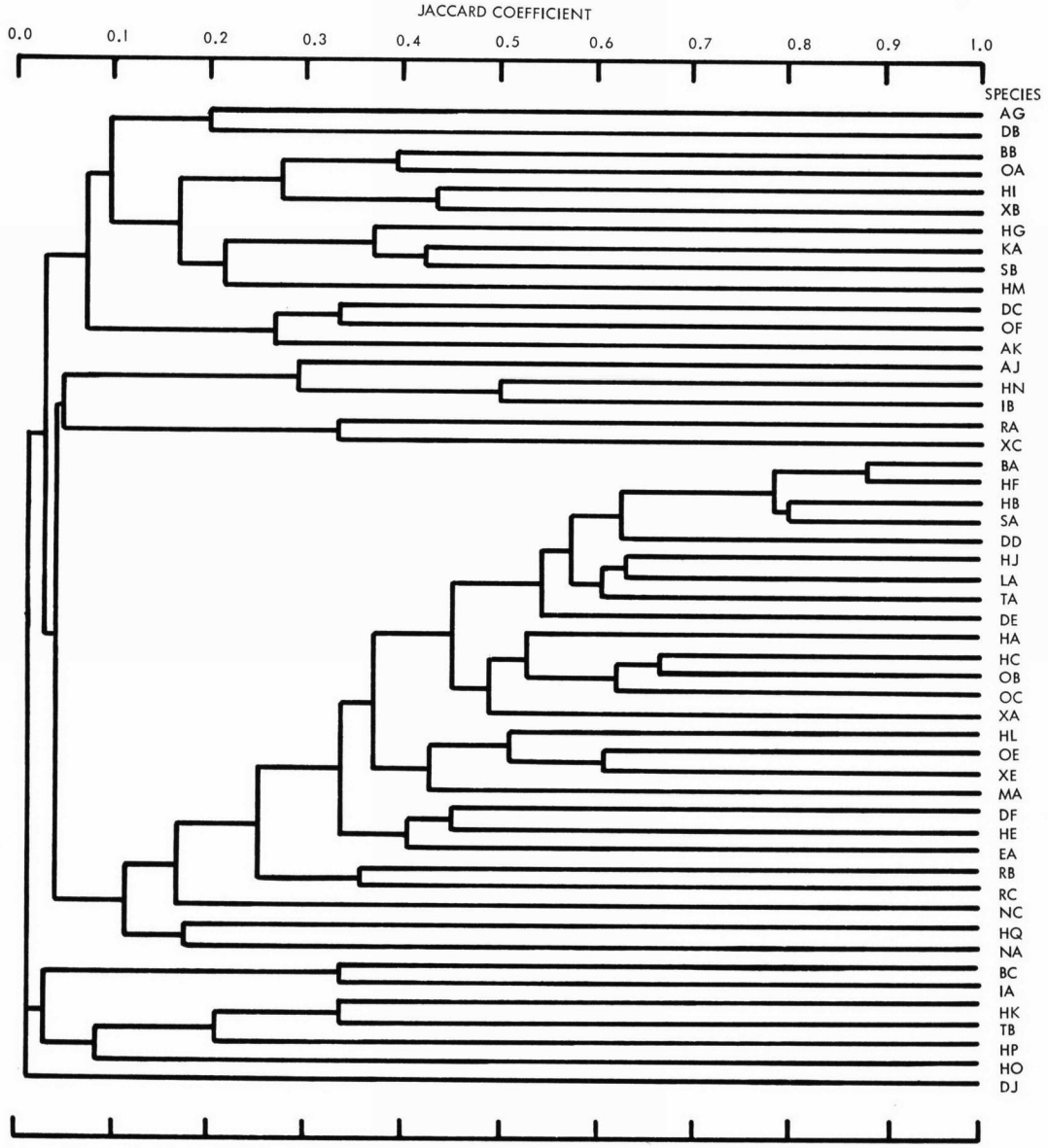


FIG. 11. Dendrogram of species associations based on the Jaccard coefficient for subfossil occurrences in the total populations of 55 sediment samples.

CORAL AND OTHER INVERTEBRATE ASSEMBLAGES

Figure 8 shows a dendrogram for species associations based on the Jaccard coefficient for occurrences in 59 live populations from living corals, sponges, ascidians, pelecypods, dead coral fragments, and algae.

Figure 6 shows a dendrogram for similarity of assemblages from corals, sponges, alcyonarians, ascidians, algae, and miscellaneous microhabitats using the Jaccard coefficient. No consistent separation of these different microhabitats is possible on the basis of the ostracode population. No assemblage can be defined as characteristic of sponges only, or of living corals as opposed to dead coral fragment accumulations, or of reef-dwelling pelecypods; these microhabitats are characterized by much the same associations. Accumulations of dead coral fragments, with their abundant encrusting algae, sponges, and microor-

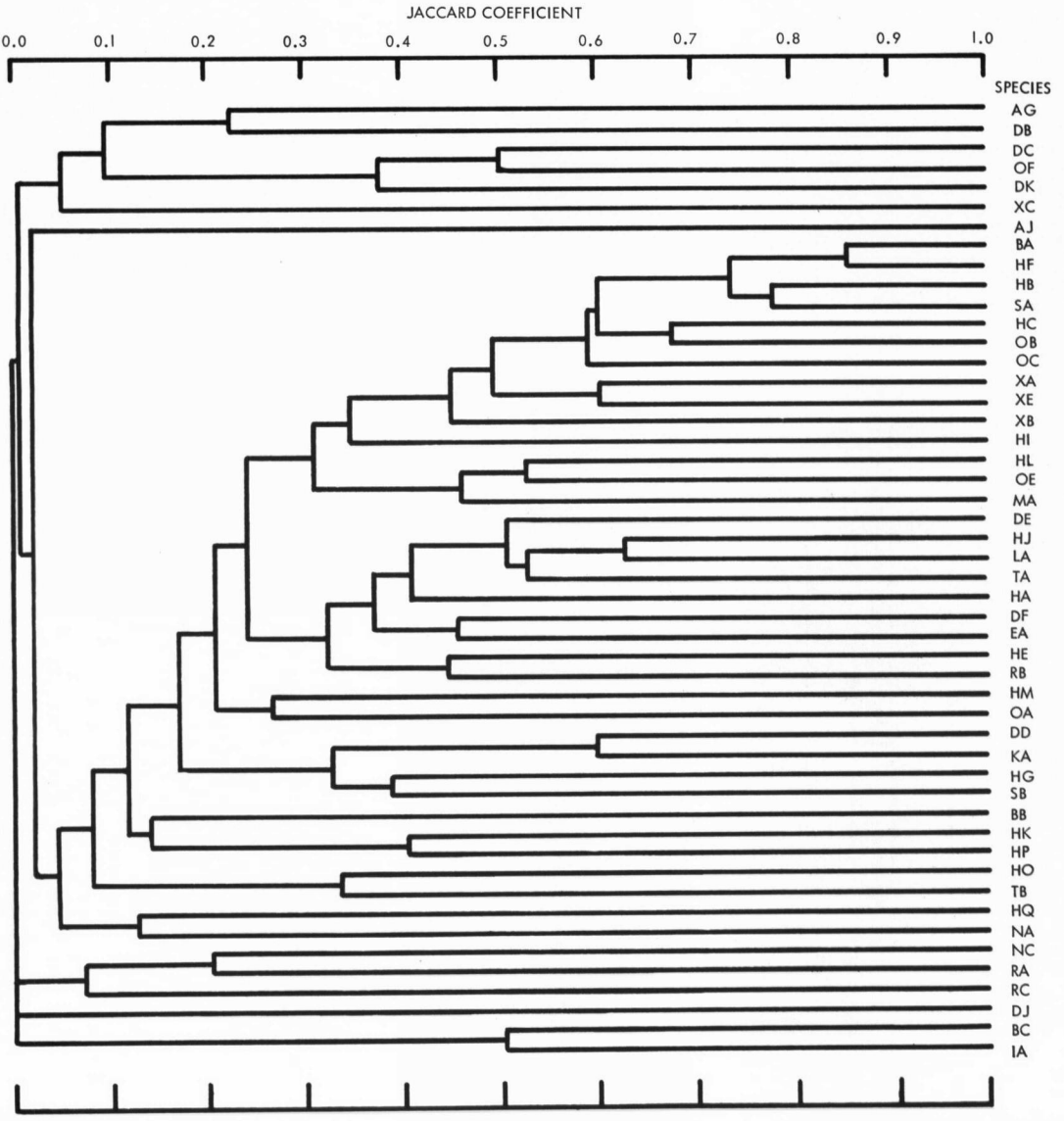


FIG. 12. Dendrogram of species associations based on the Jaccard coefficient for subfossil occurrences in the first 300 specimens picked from 55 sediment samples.

ganisms, provide abundant surface area, shelter, trapped sediment, and variety of microhabitats for small animals of all kinds. The ostracode population is large and varied, and usually it contains representatives of nearly all the species that are found in reef habitats. It is this completeness of representation rather than any peculiarity of faunal composition that accounts for the high level of association shown in the dendrogram for populations from coral fragment accumulations.

SUBSTRATE ASSEMBLAGES

Figure 9 presents the dendrogram of species associations based on the Jaccard coefficient for living occurrences in 55 sediment samples from littoral and infralittoral zones. See Table 4 for

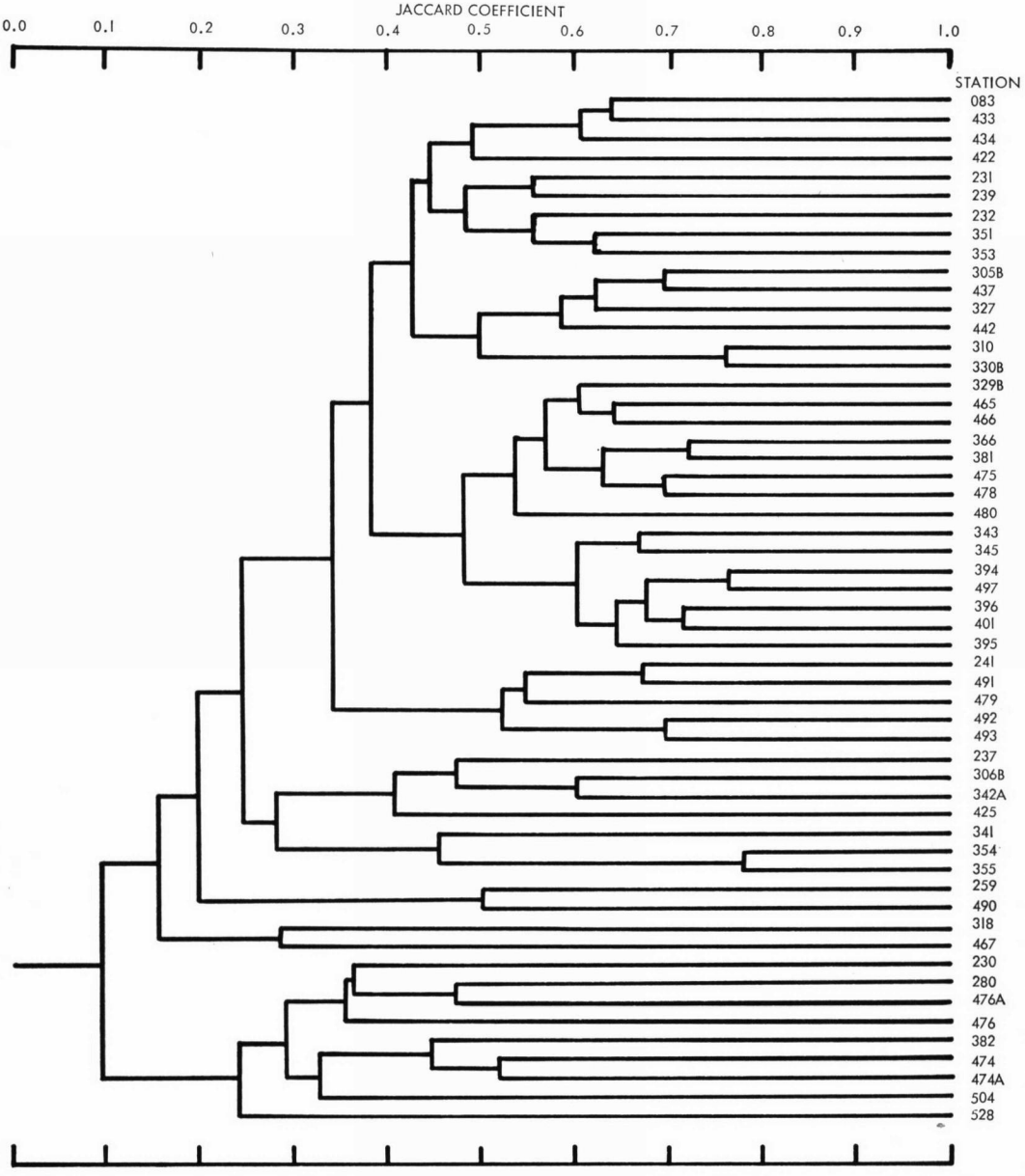


FIG. 13. Dendrogram of station similarities based on the Jaccard coefficient for subfossil occurrences in the first 300 specimens picked from 55 sediment samples.

the biofacies classification that may be derived at the 0.12 level of association from this diagram.

Figure 10 shows the dendrogram for resemblances among the 55 sediment samples on the basis of their living ostracode assemblages using the Jaccard coefficient. The biotope classification that may be derived from this diagram at the 0.09 level of similarity is summarized in Table 3, in juxtaposition with the several classifications based on subfossil assemblages.

ANALYSES OF SUBFOSSIL ASSEMBLAGES

TOTAL VIAL COUNTS

Figure 11 shows the dendrogram of species associations for subfossil occurrences in the total populations of the 55 sediment samples, using the Jaccard coefficient. See Table 4 for the biofacies classification that may be derived at the 0.15 level of similarity from this diagram.

Figure 3 presents the dendrogram of resemblances among the 55 stations based on the total subfossil populations, using the simple matching coefficient. Results for the same data, using the Jaccard coefficient, are shown in Figure 4. Possible biotope classifications derived from these diagrams are summarized in Table 3.

FIRST 300 SPECIMEN COUNTS

Figure 12 shows the dendrogram for species associations based on the occurrences among the first 300 specimens picked from the subfossil populations of the 55 sediment samples. A possible biofacies classification derived at the 0.12 level of the Jaccard coefficient is summarized in Table 4.

Figure 13 presents the dendrogram for resemblances among the 55 sediment samples on the

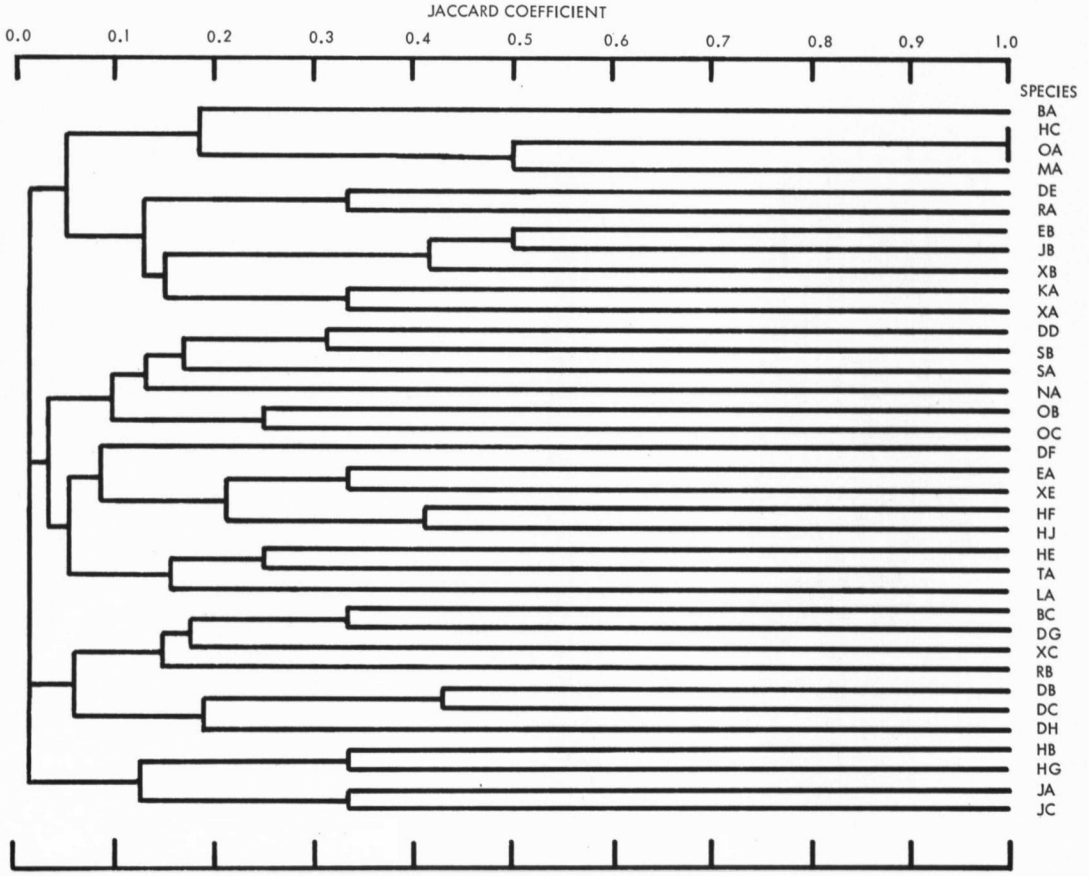


FIG. 14. Dendrogram of species associations based on the Jaccard coefficient for subfossil occurrences as intact carapaces only in the first 300 specimens picked from 55 sediment samples.

basis of the first 300 specimens picked from the fossil assemblages, using the Jaccard coefficient. A possible biotope classification derived at the 0.40 level, quite similar to that based on total populations, is summarized in Table 3.

WHOLE CARAPACE COUNTS

Figure 14 shows the dendrogram for species associations based on counts of intact carapaces only in the first 300 specimens picked, using the Jaccard coefficient. See Table 4 for the biofacies classification derived at the 0.12 level from this diagram.

Figure 15 presents the dendrogram for resemblances among the 55 sediment samples based on occurrences as intact carapaces only in the first

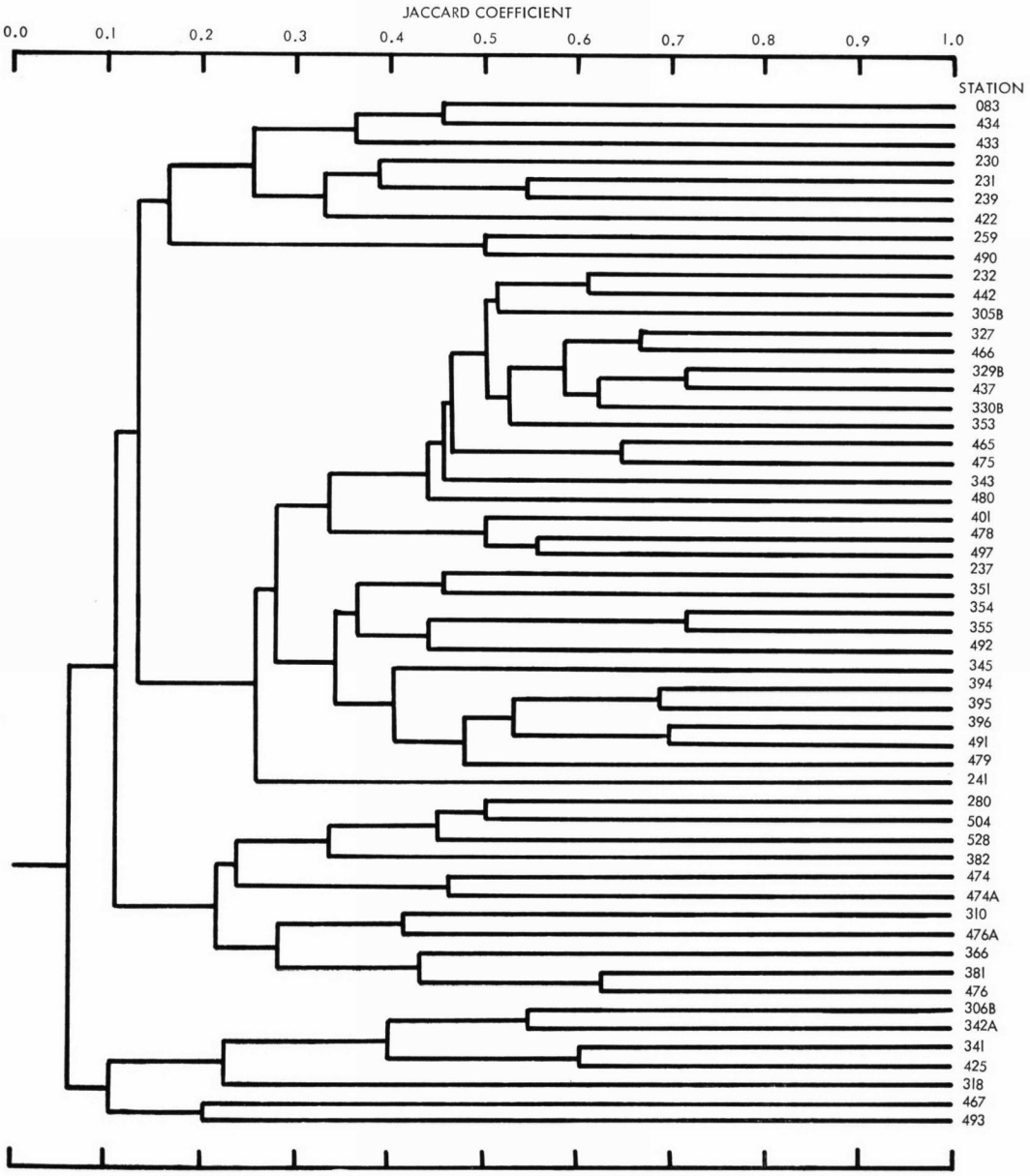


FIG. 15. Dendrogram of station similarities based on the Jaccard coefficient for subfossil occurrences as intact carapaces only in the first 300 specimens picked from 55 sediment samples.

TABLE 6.—*Derivation of Subfossil Assemblage of Intertidal Beach Sand at Ankify.*

		OSTRACODE SPECIES	SUBFOSSIL OCCURRENCES	LIVING OCCURRENCES	
				in other microhabitats	in sand
no subfossil record		AC		1	
		AD		1	
		AI		1	
		MA		2	
		EB		1	1
		JA			2
		JB			1
		JC			1
		XC			1
subfossil record	derived from local habitats	BA	6	3	
		OA	1	1	
		OB	6	6	
		OC	8	1	
		DB	2	1	1
		DC	1	4	1
		DE	4	9	1
		HA	8	1	2
		HF	7	2	4
		KA	10	2	5
		XA	4	9	4
		XB	2	10	1
		XE	2	7	1
		DD	8		4
		HG	6		1
		SA	8		2
		SB	6		3
	introduced from sublittoral habitats	DJ	1		
		HA	2		
		HI	1		
		HJ	4		
		HM	3		
		HQ	1		
		LA	1		
		OF	1		
		TA	3		
		HC	5		

Numbers represent total number of samples from which each species was recorded.

300 specimens picked. The biotope classification that may be derived at the 0.18 level of the Jaccard coefficient from this diagram is summarized in Table 3.

EVALUATION OF CLASSIFICATIONS

The biofacies classifications, summarized in Table 4, are of doubtful validity as approximations of characteristic assemblages of different biotopes. However, they describe tendencies to joint occurrence and thus suggest similar environmental needs of species.

The biotope classifications, summarized in Table 3, derived from these dendrograms constitute a workable system of classification of habitats. Grossly distinct assemblages are consistently separated; transitional assemblages and environments are arbitrarily and variably classified. The fit is best for subfossil populations; for living populations the presence or absence of one species changes the coefficient of association drastically.

The choice of coefficient controls, to some extent, the resulting biotope classification; but the patterns given by the simple matching and Jaccard coefficients are more similar to each other than are patterns derived from different sets of data. Also, the classifications based on total count and 300-count data are more similar to each other than either is to classifications based on living assemblages. The results from counting only intact carapaces agree fairly well with the other methods of subfossil classification but give no closer agreement with the classifications based on living assemblages.

COMPARISON OF LIVING AND SUBFOSSIL DISTRIBUTION PATTERNS

SPECIES COMPOSITION

Nineteen species that were found living in the Nosy Bé area have not yet been recognized in the subfossil assemblages. For the most part these are very small, fragile forms, such as most of the paradoxostomatids, or forms that are very rare in the living populations. Twelve species are represented in the subfossil assemblages for which no living examples were encountered. None of these forms is abundant, and their usual occurrence is in the large populations of muddy sands and clays from stations in deeper water. This may be their living distribution as well, but more probably this occurrence is a result of the larger populations and variety of species in these finer sediments. Their habitats in life probably are located below the littoral and reef zones where detailed sampling was possible for this study. Forty-one species were recognized in both living and subfossil states. Table 5 summarizes the living and subfossil occurrences for each species of the fauna.

CONGRUENCE OF DISTRIBUTION PATTERNS

The biofacies, or clusters of species as established by the dendrograms, do not represent entire assemblages characteristic of certain biotopes. The associations defined depend to a large extent on the species and stations included in the data. There is little correlation among these associations from one group of data to the next. In particular, the subfossil biofacies show little resemblance to those based on the living populations. Generally, the living classification is more detailed than the subfossil data permit.

None of the subfossil biotope classifications correspond well to the biotopes based on living occurrences. The results for total subfossil population, 300-count, and intact carapace data are fairly similar to one another; the dendrogram for total population (Jaccard coefficient) comes the closest but not very close to matching that for living populations. The results for Jaccard or simple matching coefficients for subfossil populations give extremely similar results.

The dendrogram for total population (Jaccard coefficient) gives the closest approximation of an *a priori* reasonable classification of environments based on such external criteria as sediment type, depth, and location. The resulting classification is very similar to that for the simple matching coefficient, which yields the most compact structure. For this reason, and because negative matches probably should be considered in the definition of subfossil biotopes, the simple matching coefficient dendrogram should be considered the basic classification of the sedimentary environments in this study.

TABLE 7.—*Derivation of Subfossil Assemblage of Intertidal Beach Sand at Antsakoabe.*

		OSTRACODE SPECIES	SUBFOSSIL OCCURRENCES	LIVING OCCURRENCES	
				in other microhabitats	in sand
no subfossil record		AA		1	
		AI		1	
		HD		2	
		JA		1	1
		JB			1
subfossil record	derived from local habitats	DB	2		1
		DD	5		2
		HG	4		1
		KA	5		3
		SA	4		2
		SB	4		3
		NA	1	1	1
		OC	5	1	1
		XA	5	6	1
		BA	5	2	
		BB	5	2	
		DC	1	1	
		DE	3	4	
		HA	3	2	
		HC	5	4	
		HI	1	2	
		OA	3	2	
		OB	5	5	
		XB	4	1	
		XE	5	3	
	introduced from sublittoral habitats	BC	1		
		DF	1		
		DK	1		
		EA	2		
		HB	4		
		HF	5		
		HJ	4		
		HK	2		
		HL	2		
		HM	2		
		HO	1		
		HP	2		
		LA	4		
		MA	2		
		OE	4		
		OF	1		
		TA	2		
		TB	1		

Numbers represent the total number of samples from which each species was recorded.

TABLE 8.—*Derivation of Subfossil Assemblage of Reef Sand at Pointe Lokobe.*

		OSTRACODE SPECIES	SUBFOSSIL OCCURRENCES	LIVING OCCURRENCES	
				in other microhabitats	in sand
no subfossil record		AA		1	
		AC		1	
		AD		1	
		AG		1	
		AH		2	
		AI		1	
		AK		1	
		HD		2	
		HE		1	
		IA		1	
		JA		1	
		JB		2	
		RA		2	
		DG			1
		XC			2
subfossil record	derived from local habitats	DB	1		1
		HF	4		2
		HI	2		2
		HJ	4		2
		MA	3		1
		RB	2		1
		BA	4	8	1
		DE	1	4	1
		HC	4	7	1
		OA	1	1	1
		BB	2	1	
		HA	3	1	
		HB	2	1	
		OB	4	6	
		XA	3	6	
		XB	2	4	
		XE	2	2	
	introduced from other habitats	BC	1		
		DC	1		
		HL	2		
		HM	2		
		OC	4		
		OE	2		
		SA	3		
		TA	1		

Numbers represent the total number of samples from which each species was recorded.

DERIVATION OF SUBFOSSIL ASSEMBLAGES

INTERTIDAL BEACH SANDS

There are three general sources for the subfossil ostracode assemblage of an intertidal sand: the living infauna and epifauna of the sand, the epifauna of grasses, algae, and other organisms within the littoral zone, and wave-introduced carapaces of forms from sublittoral habitats. All three sources can be recognized in the subfossil assemblages of the beach sands at Ankify and Antsakoabe. The species occurrence records for each of these categories are summarized for Ankify in Table 6 and for Antsakoabe in Table 7.

TABLE 9.—*Derivation of Subfossil Assemblage of Reef Sand at Ambariobe.*

		OSTRACODE SPECIES	SUBFOSSIL OCCURRENCES	LIVING OCCURRENCES	
				in other microhabitats	in sand
no subfossil record		AA		3	
		AB		1	
		AF		2	
		AI		2	
		HI		2	
		IA		1	
		JA		1	
		OA		1	
		OF		1	
		RA		1	
		BC			1
		DG			1
		DH			1
subfossil record	derived from local habitats	DC	1	1	
		DE	2	3	
		HA	2	1	
		HC	2	9	
		OB	2	4	
		XB	2	7	
		XE	1	5	
		BA	3	13	1
		DB	1	2	1
		OC	3	3	1
		XA	2	12	1
		XC	1	1	3
	introduced from other habitats	EA	1		
		HB	1		
		HF	2		
		HG	1		
		OE	1		
		SA	1		

Numbers represent the total number of samples from which each species was recorded.

TABLE 10.—*Derivation of Subfossil Assemblage of Reef Sand at Lac du Cratère.*

		OSTRACODE SPECIES	SUBFOSSIL OCCURRENCES	LIVING OCCURRENCES	
				in other microhabitats	in sand
no subfossil record		AA		1	
		AF		1	
		BC		1	
		XF		1	
		XC			1
subfossil record	derived from local habitats	DD	3		1
		EA	2		1
		HF	2		2
		HJ	1		2
		LA	3		1
		NA	1		1
		OC	2		1
		SA	3		3
		XE	3	1	1
		BA	3	3	
		DE	2	1	
		HC	2	3	
		HE	1	1	
		MA	2	3	
		OB	3	1	
		XA	3	4	
	introduced from other habitats	AG	1		
		BB	1		
		DB	2		
		DF	2		
		HA	3		
		HB	3		
		HI	3		
		HL	3		
		HM	1		
		HO	1		
		HP	2		
		KA	1		
		OA	3		
		OE	3		
		TA	2		
		XB	3		

Numbers represent the total number of samples from which each species was recorded.

CORAL REEF SANDS

The subfossil assemblages of coral reef sands derive their constituents from the infauna and epifauna of these sands; from the epifauna of grasses, algae, corals, sponges, and other organisms in the reef zone and on the rocky platform behind the reef; and from intertidal and sublittoral environments by transportation after death. Species occurrence records for these sources are summarized for Pte. Lokobe in Table 8, for Ambariobe in Table 9, and for Lac du Cratère in Table 10.

OFFSHORE SEDIMENTS

Table 11 compares living occurrences of species with their subfossil representation in the 300-count populations of 17 sediment samples. These samples include all of biotopes 4A and 5 with three stations from biotope 3 of the biotope classification based on Figure 3 (for simple matching coefficient based on total number of specimens picked). The sediment types represented, summarized in Table 3, include carbonate sand, quartz-carbonate sand and sandy mud of varying compositions, and clay. Depths range from 2 to 30 m. It is apparent from this table that the greatest subfossil abundance of a species does not necessarily correspond with its living distribution, and conversely that a species may leave no subfossil record in the sediment it inhabits.

Few generalizations are possible from these data. Species HF and HJ are most commonly found living in quartz carbonate sands and sandy muds; their robust carapaces are abundant constituents of sands of many types. Species LA, EA, and DF prefer finer sediments; their smooth carapaces are less significant contributors to subfossil populations.

Specimens of shallow-water and intertidal species may be transported into the deeper water sediments; their presence and abundance depends on the distance from the source of supply, such as corals or the mouth of a river, and on the resistance of the carapace to breakage in transport. Some clays have a large representation of thin-shelled smooth species, as a result of the more buoyant nature of these specimens and of the favorable low energy conditions. For example, carapaces of species DE, which is a very common intertidal and shallow water form on algae and dead coral fragments and occasionally occurs living in sublittoral carbonate sands, are extremely abundant in the subfossil populations of samples 492 and 493 (clay at 10 and 30 m.). Similarly, species DD, characteristically an intertidal sand- and mud-dweller, is an important subfossil constituent at the stations of biotope 4A (clays at 10 to 30 m.).

RECOGNITION OF INDIGENOUS SPECIES

The difficulty of distinguishing recently living specimens even in freshly collected sediment samples has been discussed on foregoing pages. The distinction of indigenous species from exotic species in subfossil assemblages is even more problematical, and as yet no infallible criteria can be proposed.

The proportion of intact carapaces has been demonstrated to be a property characteristic of an individual species that does not vary significantly among stations and appears not to be greatly affected by transportation of specimens into a new locality. The results of analysis by χ^2 of intact carapace to single valve ratios for several species showed no significant differences between stations where the species occurred both living and subfossil and stations where it occurred subfossil only. Similar non-significant results were obtained for the proportions of left and right valves among single valve specimens of a species at different stations. The distribution of intact carapaces does not approximate the distribution of living specimens any better than that of the total count of subfossil specimens.

Clarity of the carapace and abundance of fragmentary specimens were not examined systematically, but no general trends were apparent. Both properties appear to be specific to a given species rather than to the locality of collection. Blackening of a carapace, similar to that observable on skeletal fragments of many kinds in some carbonate sands, appears to indicate diagenetic effects of the oxygen-deficient zone of the sediment. However, one such blackened specimen of species HF from station 466 was very much alive and moving when captured!

Relative abundance of species in subfossil populations may be a clue to distinguishing indigenous species. In populations from littoral and sublittoral carbonate sands the species that live in or

on the sand or that live on plants, corals, or other organisms in the immediate area almost always are the most abundant forms in the subfossil population. Introduced specimens of exotic species are very much less abundant. But in the finer offshore sediment, especially away from the areas of coral growth, the relatively few species actually living in the sediment may or may not contribute greatly to its subfossil population.

For several common species an attempt was made to compute a discriminant function equation to distinguish between stations where the species was found both living and subfossil and stations where it occurred subfossil only. The two ratios measured, intact carapaces/total number of specimens of species and total specimens of species/total subfossil population of fauna, after arcsin $\sqrt{\times}$ transformation, did not yield an equation that would adequately distinguish the two populations.

TABLE 11.—*Comparison of Living Occurrences with Subfossil Representation in 300-Count Populations of 17 Samples of Offshore Sediments.*

	Biotope 5									Biotope 4A				Biotope 3			
	491	479	396	345	497	401	395	394	343	493	355	354	492	241	478	480	353
AJ										10							
BA	11	1	14	9	29	58	8	18	48				1	32	*48*	*40*	15
BC																2	
DB									—								
DD			1	1		4			33	40	78	110	25				27
DE	3	4	6	3	2	9	13	1	21	90			146	1		2	3
DF	*39*		*4*		*20*	*15*	—		*15*					*22*	1	1	
EA	*35*		*7*	*8*	47	35	11	*10*			2		7	26		4	
HA			3	4	27	21	2	2	3					1	4	20	
HB	8	21	6	8	35	37	11	5	15	40	33	40	36	5	18	11	6
HC				1			2	1	3						2	2	
HE	1		1	5	17	15	*8*	3	6						6	*6*	27
HF	6	*65*	*66*	23	2	1	*126*	*10*	9				4		3	8	*30*
HI															1		
HJ	42	*46*	*65*	*112*	20	11	*9*	*81*	33	10	1	4	35	27	*121*	162	*72*
HL		1					1								5	1	
HM		5	5				24	1									6
HQ											2	17					3
IA																	2
KA									3								
LA	7	1	8	4	11	14	*6*	7	30	10	*10*	*11*	*9*	2	2		3
MA	25		1		8	15	1	1							1	4	—
NA	1	3	—							*20*			18	13			6
NC		2	1			1								1	3		
OA									12								
OB				1					18			1					
OC					4			1							5		
OE		1				1	1		15						5	2	
RA															1		
RB				3	3	6	1	4	9	30			4		20		
SA	72	122	87	77	40	16	54	107	*26*	50	112	*76*	*37*	118	27	36	60
TA	55	28	25	39	25	31	*15*	35	6	20	60	40	13	*51*			
XA					5	11		2							1	5	3
XB															1	1	6
XC					1											—	
XE						5	8	*5*	6						1	4	3
DEPTH	10	15	10	14	20	23	11	14	2	30	17	15	10	10	10	15	10
TOTAL SAMPLE POPULATION:	2234	527	1565	1502	780	677	469	1698	110	320	2070	1337	336	3007	719	323	93

Numbers represent the number of subfossil specimens recorded in the 300-count populations of each station. Italicized counts indicate stations where species was found living.

PALEOECOLOGICAL INTERPRETATION

The results of comparing subfossil with living distributions in the Nosy Bé area show that for littoral and nearshore sublittoral environments the subfossil ostracode populations are generally representative in composition of the living ostracode assemblages in the immediate area. However, the coarseness of scale at which habitats may be distinguished by their characteristic assemblages is much greater for subfossil faunas than for living forms, because a single sedimentary environment receives carapaces from several distinct life microhabitats. Mixing, dispersion, and differential removal of species blur the previously sharp contrasts between assemblages. The resulting associations and proportions in the subfossil fauna do not correspond exactly to any of the several contributing life associations, but they are representative of the area as a whole and may be

distinguished from comparable accumulations in other environments.

The subfossil assemblages of offshore sandy muds and clays from deeper water, more likely to be preserved in the geologic column than those of littoral and shallow water zones, are less distinctive. They contain elements not only of the indigenous species but also of nearby littoral and shallow-water sublittoral environments, in proportions dependent more on energy level and resistance of species to abrasion than the original abundance. These subfossil assemblages may be said to be representative of a life association only in a broad regional sense. As the long-term average of the several local environments, these faunas are more easily interpreted in geologic terms than those of more localized and ephemeral habitats.

Because the relationships of the subfossil assemblages to the indigenous living populations are attenuated and obscure, paleoecological interpretation of a subfossil assemblage can be made most efficiently by direct comparison of subfossil distribution patterns with external ecological and physical parameters of the area. The usefulness of the micropaleontological-paleoecological investigations of Recent ostracode populations probably has not been significantly impaired by their failure to consider the living distributions of ostracode species.

SYSTEMATIC DESCRIPTIONS

Ostracode species indicated by arbitrarily chosen letter designations are described under families as defined in the *Treatise on Invertebrate Paleontology* (Part Q, 1961) to which they are presumed to belong. Notes on observed variations within each species are included wherever pertinent. Its inferred habitat or subfossil occurrences (if known), or both are reported. Type specimens have been deposited in the University of Kansas Museum of Invertebrate Paleontology, where they may be found readily under their assigned letter symbols without need for publishing catalog numbers here. Abbreviations used include C, carapace; H, height; L, length; loc., collecting localities listed with numbers and descriptions on p. 6; LV, left valve; RV, right valve; sta., station; T, thickness; W, width.

TABLE 12.—*Key to Algal Species Code Designations.*

COLOR	CALCAREOUS	GROWTH HABIT	SPECIES CODE
Green			
	Calcareous		
		Halimeda-type	F
		Bossea-type	I, X
	Noncalcareous		
		fine tangled filamentous clumps	A
		fine fibrous or branching clusters, encrusting	V, BK, BR
Red			
	Calcareous		
		Galaxaura-type	E
		Amphiroa-type	W
		Lithothrix-type	CB
	Noncalcareous		
		Acanthophora-type	J
		Callophyllis-type	Q, BU
		Digenia-type	BH, BM, BO

Bar-ended lines accompanying ostracode illustrations in this paper indicate length of 0.1 mm.

For convenience, the alphabetically arranged list of species letter designations in Table 5 shows pages on which descriptions are published. An explanation of letter symbols adopted for host species of algae associated with occurrence of Nosy Bé ostracodes is given in Table 12.

Family PARADOXOSTOMATIDAE Brady & Norman, 1889

Genus UNCERTAIN

Species AA

Carapace compressed, elongate, only slightly higher posteriorly than anteriorly, usually lacking caudal process or posterodorsal sinuosity, ventral margin faintly sinuous. Carapace colorless and transparent; body faintly greenish, eyes red-brown.

Remarks.—Continuous variation seemingly connects this form and sp. AI, which has a distinct caudal process and more arched posterodorsal margin; intermediate forms probably not classified consistently.

Type.—Adult male collected living at sta. 219 (Fig. 16,*1*). It lacks caudal process. L, 0.59 mm.; H, 0.23 mm.

Habitat.—Specimens recovered from washings of many varieties of algae and *Cymodocea*, as well as from living corals, accumulations of dead coral fragments, and reef-dwelling bivalves.

Species AB

Carapace very elongate and compressed, dorsal margin nearly straight, ventral margin arcuate,

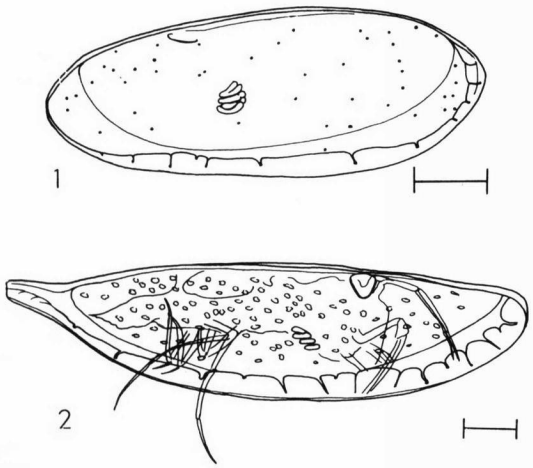


FIG. 16.—*1*. Species AA, interior of right valve.—*2*. Species AB, right exterior of whole specimen showing small brown spots on the carapace.

caudal process very attenuate. Carapace of preserved specimen transparent white, marginal areas clear, lateral area with small light-brown spots; body and appendages yellow, eyes red.

Type.—Female collected living at sta. 159 (Fig. 16,*2*). L, 0.95 mm.; H, 0.26 mm.

Habitat.—Found on living corals at locs. 1 and 12 and on an alcyonarian at loc. 14.

Species AC

Carapace small, compressed, with dorsal margin broadly arched, anterior and posterior margins broadly and very nearly equally rounded, ventral margin only very slightly sinuous, without any trace of caudal process or posterodorsal sinuosity. Living specimens mottled black with clear margins, eye dark red, body and appendages yellow.

Type.—Black male specimen from sta. 220 (Fig. 17,*1*). L, 0.47 mm.; H, 0.21 mm.

Habitat.—Specimens found in washings of algae, *Cymodocea*, living corals, and dead coral fragments from locs. 5, 6, 11, 12, 13, and 14.

Species AD

Carapace moderately inflated, anterior margin narrowly rounded, posterior margin broadly rounded, ventral margin strongly indented considerably anterior to mid-length. Radial pore canals rather numerous, straight, thick; normal pore canals simple, fairly large. Living specimens yellow, about one-fourth of area covered by irregular reddish brown patches; body and appendages yellow.

Type.—Adult male from sta. 67 (Fig. 17,*2*). RV L, 0.45 mm.; H, 0.19 mm.

Habitat.—Found in washings of *Cymodocea* and three kinds of algae from locs. 11, 12, and of *Thallassia* from loc. 5.

Species AE

Carapace soft, similar in shape to sp. AF but more inflated, anterior margin more broadly rounded, posterior margin less angularly truncate; also similar to sp. AG except smaller, more elongate, and less inflated. Living specimen pale yellow with two narrow vertical bands of pale brown color; body and appendages yellow, eye red. Lacks black body of sp. AF and pattern marking of sp. AG.

Remarks.—This species was erected to accommodate a single anomalous specimen from sta. 56. It may be an immature individual of sp. AG.

Type.—Specimen collected living from sta. 056 (Fig. 18,*1*). L, 0.37 mm.; H, 0.20 mm.

Habitat.—Found in washings of alga type E from loc. 11.

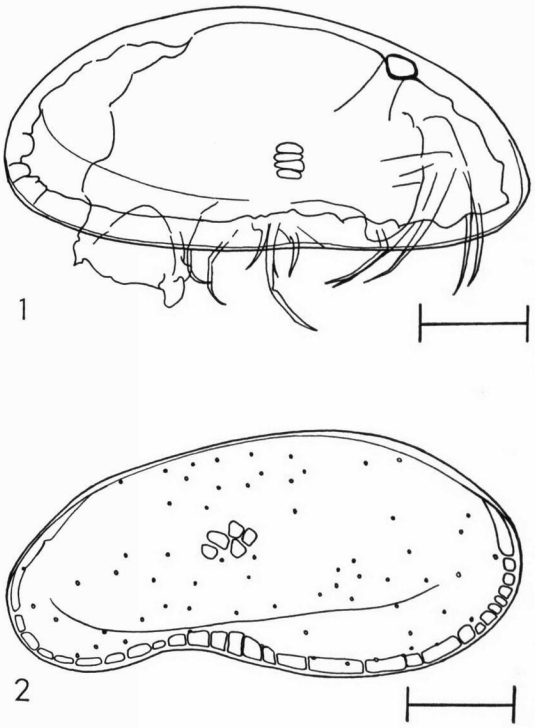


FIG. 17.—*1*. Species AC, right exterior of whole specimen. —*2*. Species AD, interior of right valve.

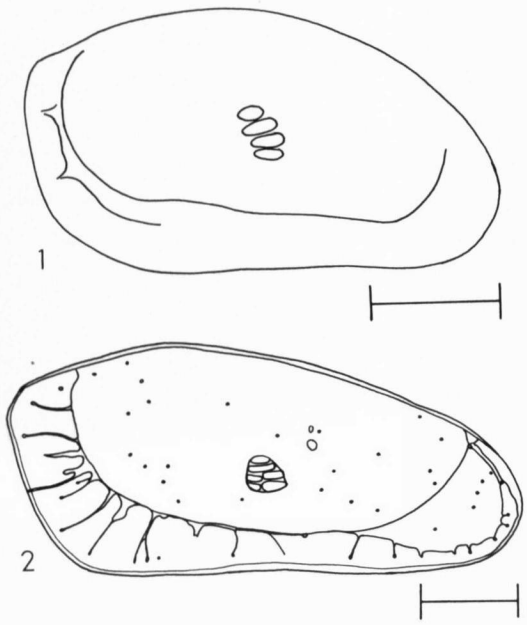


FIG. 18.—*1*. Species AE, right exterior of whole specimen. —*2*. Species AF, interior of left valve.

Species AF

Carapace small, smooth, centrally somewhat inflated, marginally compressed. Anterior margin narrowly rounded, dorsal margin arching steeply upward to highest point near posterior end; posterior end bluntly truncated, posterior margin straight, meeting ventral margin at distinct slightly obtuse angle; posterodorsal angle slightly sinuate. Duplicature very wide, anterior vestibule deep, posterior duplicature entirely fused, with no vestibule. Radial pore canals fairly numerous, curving, widened proximally, most terminating at normal pore canals within zone of concrescence and not reaching margin. Body of living specimens is black centrally and dorsally, yellow in anterior, ventral, and posterior areas; appendages yellow, eye dark red, carapace transparent and yellowish.

Remarks.—Some individuals of the very variable sp. AI closely resemble sp. AF in lateral outline, but their posteroventral angle is not as sharply defined. No males were found among specimens of sp. AF.

Type.—Adult female collected living at sta. 188 (Fig. 18,2). LV L, 0.50 mm.; H, 0.23 mm.

Habitat.—Alga-encrusted surfaces of living corals, dead coral fragments, *Tridacna*, algae types E and Q, at locs. 1, 9, 11, 12, and 14.

Species AG

Carapace subovate, moderately inflated, without caudal process, sinuosity of ventral margin not pronounced. Duplicature very wide, vestibule wide and continuous, radial pore canals few in number. Hinge weakly lophodont, in right valve consisting of ventrally directed simple anterior and posterior teeth connected by a shallow groove. Carapace of living form medium brown except for clear margins and two irregularly defined narrow vertical clear streaks; subfossil carapace white, retaining irregular pattern as transparent areas; body and appendages yellow, eyes not conspicuous.

Type.—Adult male collected living at sta. 514 (Fig. 19). L, 0.65 mm.; H, 0.38 mm.

Habitat.—Living specimens found in washings of several types of algae and of dead coral fragments at locs. 3, 6, 10, 11, 12, and 13.

Subfossil distribution.—Calcareous intertidal and reef sands from locs. 1, 9, and 11.

Species AH

Carapace soft, similar in lateral outline to species AF but larger and more inflated, smaller than species AL and lacking extended caudal

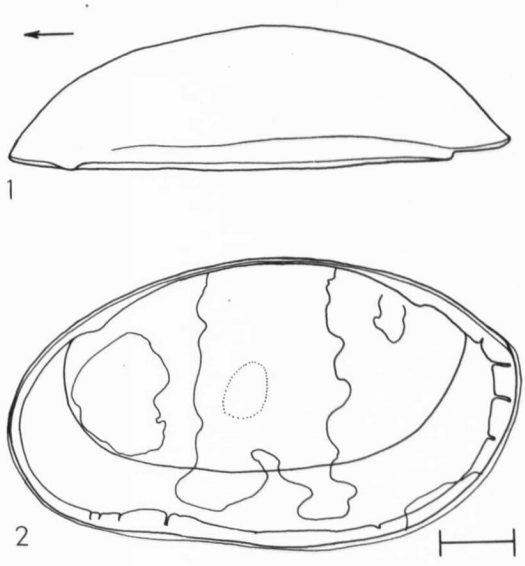


FIG. 19. Species AG.—*1*. Dorsal view of right valve.—*2*. Interior of right valve showing pattern of brown and clear areas.

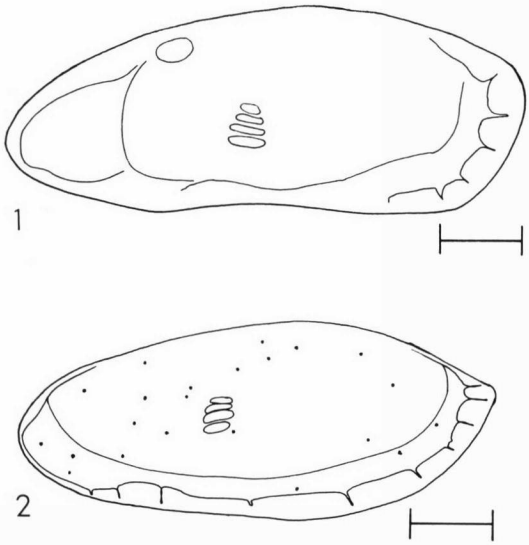


FIG. 20.—*1*. Species AH, left exterior of whole specimen. —*2*. Species AI, interior of right valve.

process. Carapace of preserved specimen translucent white, body yellow and black, appendages yellow, eyes red.

Remarks.—This category is created for four specimens that could not be assigned with certainty to the better defined paradoxostomatid species AA, AF, or AL.

Type.—Male collected living at sta. 093 (Fig. 20,*1*). L, 0.61 mm.; H, 0.25 mm.

Habitat.—Specimens found in washings of alga type W at loc. 13, and of living and dead coral masses at locs. 13 and 14.

Species AI

Carapace similar in shape and size to species AA but not as elongate and with variably developed caudal process. Carapace of living form transparent, body pale yellow, eyes red.

Remarks.—Rather great variability of this species results in forms distinguishable only with difficulty from species AA and AF.

Type.—Adult male collected living from sta. 295 (Fig. 20,2). RV L, 0.57 mm.; H, 0.24 mm.

Habitat.—Specimens collected from many types of algae, *Cymodocea*, living coral, reef-dwelling pelecypods, dead coral fragments, and a solitary red ascidian, at nearly all shore collecting localities.

Species AJ

Carapace large, elongate, moderately inflated, anterior and posterior margins narrowly and nearly equally rounded, dorsal margin broadly arched, highest at midlength, ventral margin sinuous.

Type.—LV collected subfossil from sta. 497 (Fig. 21,*1*). L, 0.77 mm.; H, 0.28 mm.; W, 0.23 mm.

Habitat.—A single living specimen tentatively assigned to this species was found in washings of dead coral fragments from loc. 11.

Subfossil distribution.—Soft clay with oyster fragments at 10 m., clay at 30 m., Baie d'Ampasindava; muddy sand at 20 and 27 m., south of Hellville.

Species AK

Carapace small, elongate, dorsal margin broadly arched, anterior and posterior margins narrowly and nearly equally rounded, ventral margin somewhat convex and irregularly sinuate. Carapace of preserved specimen translucent white, body yellow with black streaks, appendages yellow, eyes red.

Remarks.—Category based on single specimen from station 376 with singular shape. Much smaller and relatively more inflated than species AJ, but may represent immature stage.

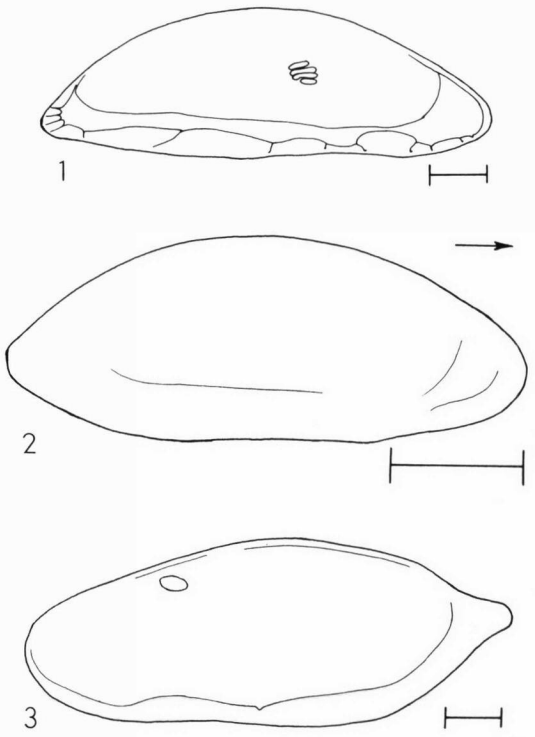


FIG. 21.—*1*. Species AJ, interior of left valve.—*2*. Species AK, right exterior of whole specimen.—*3*. Species AL, left exterior of whole specimen.

Type.—Single specimen collected living from sta. 376 (Fig. 21,2). L, 0.38 mm.; H, 0.16 mm.

Habitat.—Only specimen recovered from washings of alga type W from loc. 13.

Species AL

Large, moderately inflated paradoxostomatid with much extended caudal process; carapace soft. Carapace of preserved specimen translucent white, body and appendages yellow, eyes red.

Remarks.—Category based on single specimen from station 514.

Type.—Female collected living at sta. 514 (Fig. 21,*3*).

Habitat.—Only specimen found in washings of alga type BH from loc. 3.

Family BAIRDIIDAE Sars, 1888

Genus BAIRDIA M'Coy, 1844

Species BA

Carapace conventional bairdiid shape, posterior angle somewhat acuminate, bearing a single terminal spine; anterodorsal and posteroventral margins variably spinose. External surface occasionally smooth but usually very finely punctate. Living specimens and recently molted carapaces bear abundant coarse brown bristles; near posterior end siphonate projection formed by fusion of several long bristles. Color pattern of carapace quite variable. Living specimens range from entirely creamy white, to white with irregular brown areas, to mottled pattern of about half brown and half white, to rare forms entirely unevenly dark brown. Subfossil carapaces white, rarely retaining traces of pattern as transparent areas. Bristles dark brown, body and proximal parts of appendages yellow, distal segments of appendages black.

Remarks.—Considerable variability apparent in color pattern, discernible differences in lateral outline, marginal denticulation, and surface pitting. At least two species have been included in this heterogeneous category.

Type.—Adult male collected living from sta. 212 (Fig. 22). Specimen about half brown and half white; central area outlined by dots subopaque white. LV L, 1.06 mm.; H, 0.55 m.; RV L, 1.04 mm.; H, 0.50 mm.

Habitat.—Extremely common on surfaces of all types of organisms, especially reef corals, also sponges, alcyonarians, a solitary red ascidian, reef-dwelling pelecypods, *Millepora*, both polyp surfaces and porous encrusted bases of living reef corals, dead coral fragments, most varieties of algae, *Cymodocea*, *Syringodium*, and other grasses. More rarely encountered in sands among reef corals or in *Cymodocea* beds, low tide level to 15 m. depth; one specimen recorded from soft clay containing oyster shells at 10 m. in the Baie d'Ampasindava.

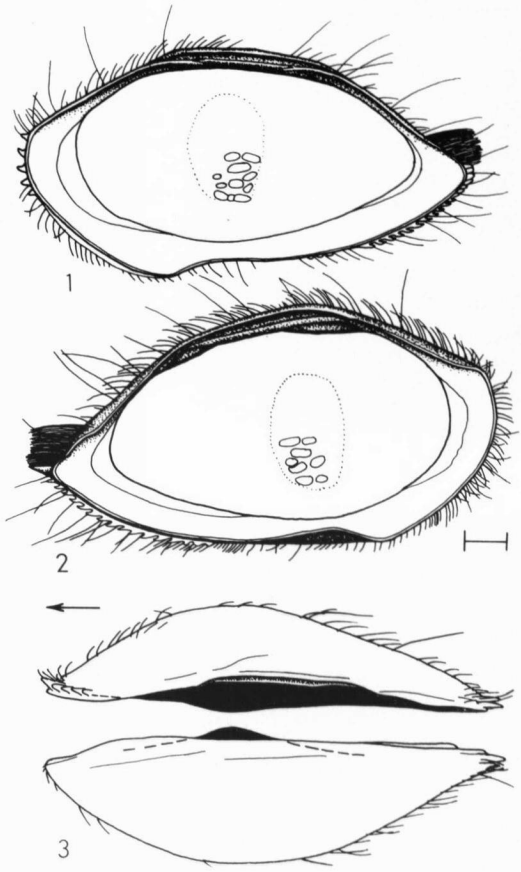


FIG. 22. Species BA.—*1*. Interior of right valve.—*2*. Interior of left valve.—*3*. Dorsal view of both valves.

Subfossil distribution.—Present in nearly every type of marine sediment and all localities in study area; only sediments consistently lacking this form are intertidal mud banks along mangrove-lined estuarine channels of locs. 8 and 15. Especially abundant in channel sands of Passe de Nosy Vorona and in the coarse reef and fore-reef carbonate sands at locs. 1, 2, 9, 12, 13 and 14; common in carbonate sands from *Cymodocea* and dead coral fragment banks of locs. 3, 10, 11, and 13; less abundant in intertidal quartzose and carbonate beach sands of locs. 5 and 16, carbonate and quartz-carbonate sands south and east of Nosy Komba and south of Hellville; persistently present in negligible frequencies in sands, muds, and clays of nearly all collections.

Species BC

Carapace smooth, compressed, lateral outline subreniform; hinge thin but well developed, muscle scar pattern an aggregate of distinct raised scars. Living specimen with abundant short

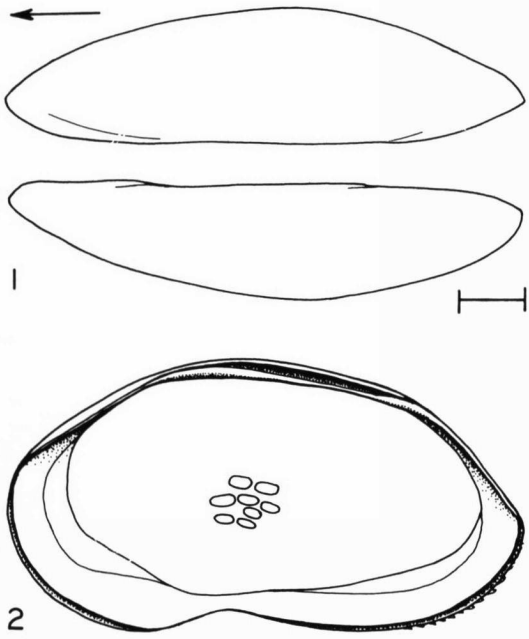


FIG. 23. Species BC.—*1*. Dorsal view of both valves.—*2*. Interior of right valve.

brown bristles; posteroventral margin with tiny denticles. Carapace of most living specimens uniformly dark brown except for clear margins and small irregular white patches in central area. Subfossil carapaces may retain traces of this color pattern. Body colorless, appendages and genital lobes becoming dark brown distally, selvage and bristles dark brown.

Remarks.—No male specimens of this species were found.

Type.—Adult female collected living from sta. 219 (Fig. 23). RV L, 0.77 mm.; H, 0.41 mm.

Habitat.—Collected from washings of dead coral fragments at locs. 9 and 12, from sand among coral masses at loc. 1.

Subfossil distribution.—Sparsely represented in carbonate sands of locs. 1, 9, 11, 13, 16, and east of Nosy Komba.

Genus TRIEBELINA van den Bold, 1946

Species BB

Carapace small but very robust, covered with closely spaced steep-walled pits, bearing thick pitted dorsal and ventrolateral ridges and shorter median ridge. Lateral outline subtrapezoidal, with horizontal dorsal and ventral margins, posterodorsal angle nearly right angle; margins with thick irregularly spaced denticles. Hinge consisting of narrow groove in left valve, thin bar and accommodation groove in right valve. Carapace of living specimen opaque white with sparse brown bristles, brown selvage and hinge structures. Body colorless, appendages brown.

Type.—Adult male collected living from sta. 159 (Fig. 24). LV L, 0.61 mm.; H, 0.34 mm.; W, 0.20 mm.; RV L, 0.61 mm.; H, 0.29 mm.; W, 0.20 mm.

Habitat.—Found on living corals and dead coral fragments at locs. 1, 3, and 12.

Subfossil distribution.—Sparsely represented in carbonate sands at locs. 1, 9, 11, 13, 16, and south of Hellville.

Family PONTOCYPRIDIDAE G. W. Müller, 1894

Genus PONTOCYPRIA G. W. Müller, 1894

Species DA

Carapace suboval in lateral view, thickest and highest anteromedially; smooth with extremely

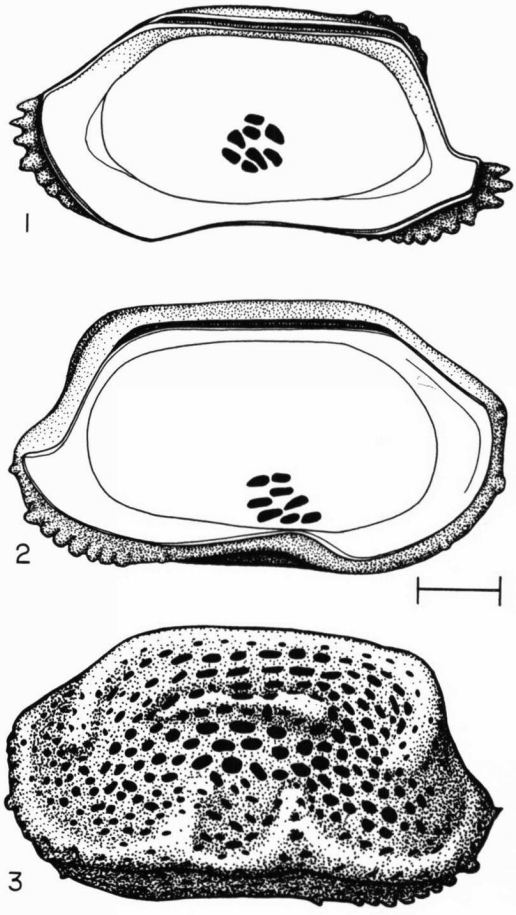


FIG. 24. Species BB.—*1*. Interior of right valve.—*2*. Interior of left valve.—*3*. Exterior of left valve.

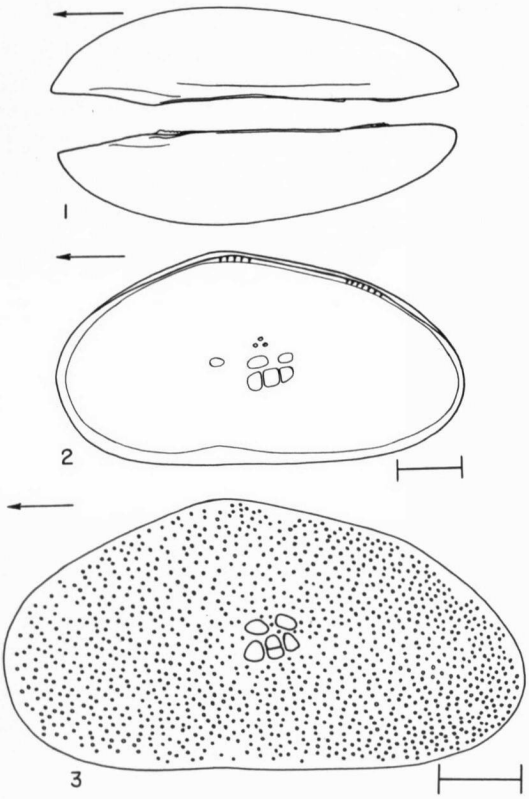


FIG. 25. Species DA.—*1*. Dorsal view of both valves.—*2*. Interior of right valve.—*3*. Exterior of left valve.

numerous normal pore canals visible as pits. Hinge very narrow, three-part, terminal elements faintly crenulate. Muscle-scar pattern an aggregate of five large scars, three ventral and two dorsal. No radial pore canals visible. Ejaculatory tubes of male of simple tubular structure. Carapace of living specimen yellowish white with light brown bristles and margins; body pale yellow.

Type.—Adult male specimen collected living at sta. 508 (Fig. 25). LV L, 0.61 mm.; H, 0.32 mm.; RV L, 0.62 mm.; H, 0.38 mm.

Habitat.—Only recorded occurrence in washings of large sponge collected from depth of 20 m. at loc. 12.

Genus PROPONTOCYPRIS Sylvester-Bradley, 1947

Species DC

Carapace moderately inflated, thickest medially; dorsal margin broadly arched, highest at midlength; anterior margin broadly rounded, ventral margin only slightly sinuate, posterior not acuminate. Zone of concrescence narrow, traversed by abundant straight radial pore canals. Normal pore canals numerous, small. Ejaculatory tubes of male simple tubular structures. Carapace colorless, except for brown chitinous edging of margins, body pale yellow.

Type.—Adult male collected living from sta. 082 (Fig. 26). RV L, 0.78 mm.; H, 0.40 mm.

Habitat.—Abundant in washings of alga type A from locs. 1 and 5, also found there on sponges and *Syringodium*; present in washings of dead coral fragments from loc. 12, intertidal beach sand from loc. 6, and carbonate sand from *Cymodocea* beds at loc. 3.

Subfossil distribution.—Reef and intertidal beach sands from locs. 1, 5, 13, and 16.

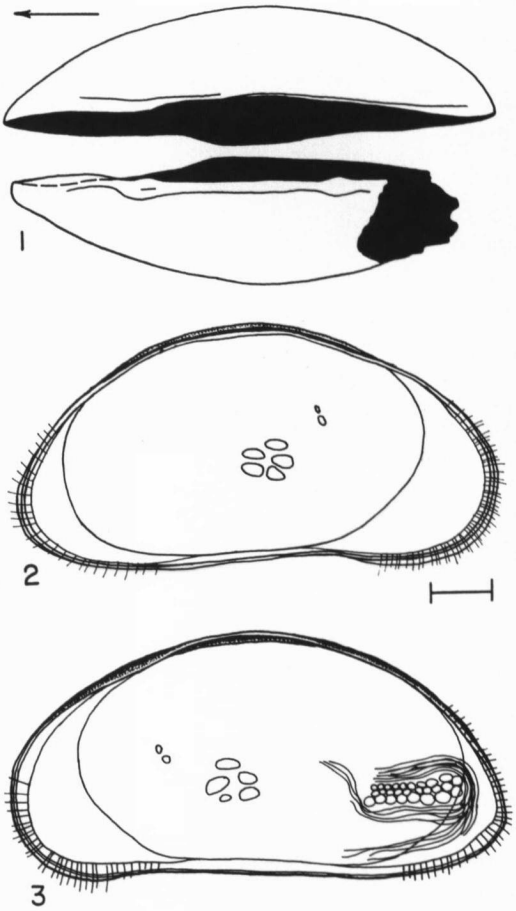


FIG. 26. Species DC.—*1*. Dorsal view of both valves.—*2*. Interior of left valve.—*3*. Interior of right valve, showing soft remnants of testes between the inner and outer lamellae.

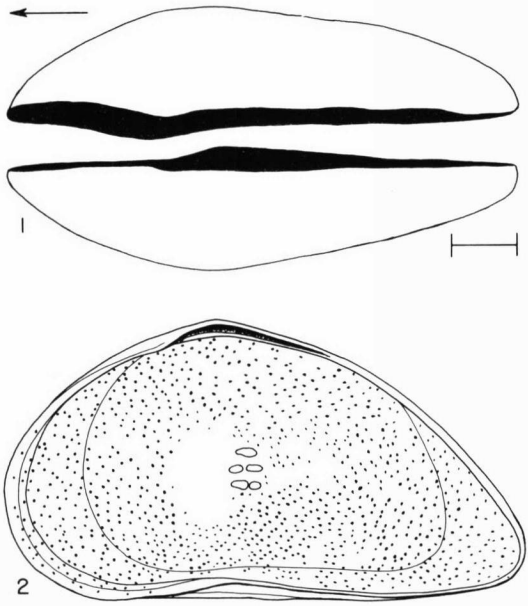


FIG. 27. Species DE.—*1*. Dorsal view of both valves.—*2*. Interior of left valve.

Species DE

Carapace smooth, moderately inflated, highest and thickest anterior to midlength, dorsal margin highly arched and angular, posterior end acuminate. Normal pore canals very small and numerous, each with short thin brown bristle, radial pore canals indistinct or not differentiated. Hinge adont. Carapace of living specimen transparent yellowish, body yellow with brown spots, appendages yellow.

Type.—Adult male collected living at sta. 082 (Fig. 27). LV L, 0.77 mm.; H, 0.41 mm.; RV L, 0.77 m.; H, 0.42 mm.

Habitat.—Common on many varieties of calcareous and noncalcareous algae, *Thallassia*, and dead coral fragment and shell accumulations at all shore localities; also reported living in intertidal beach sand at loc. 5.

Subfossil distribution.—Specimens of this species were especially abundant in samples of carbonate sands from loc. 9 and of soft clay with oyster fragments in the Baie d'Ampasindava. Otherwise widely distributed but never abundant in carbonate and quartz-carbonate sands and muds from many localities.

Family PARACYPRIDIDAE Sars, 1923

Genus AGLAIOCYPRIS Sylvester-Bradley, 1946

Species DB

Carapace smooth, unusually compressed, anterior margin bluntly rounded, posterior outline narrowly rounded, dorsal margin arched, highest point anterior to midlength. Duplicature and vestibules very broad, radial pore canals thin and straight, fairly numerous. Zenckers organs of male carrying six whorls of radiating spikes. Coloration extremely variable. At certain stations specimens completely white, with faintly yellowish body and appendages. Carapace more commonly light mottled brown. At sta. 326 and 421, specimens very colorful, with completely transparent carapace, bright yellow body and appendages, and brilliant maroon patches over about one-third lateral area of inner lamella. Subfossil carapaces generally translucent white.

Remarks.—Carapace morphology of colorful variants does not differ significantly from that of colorless forms.

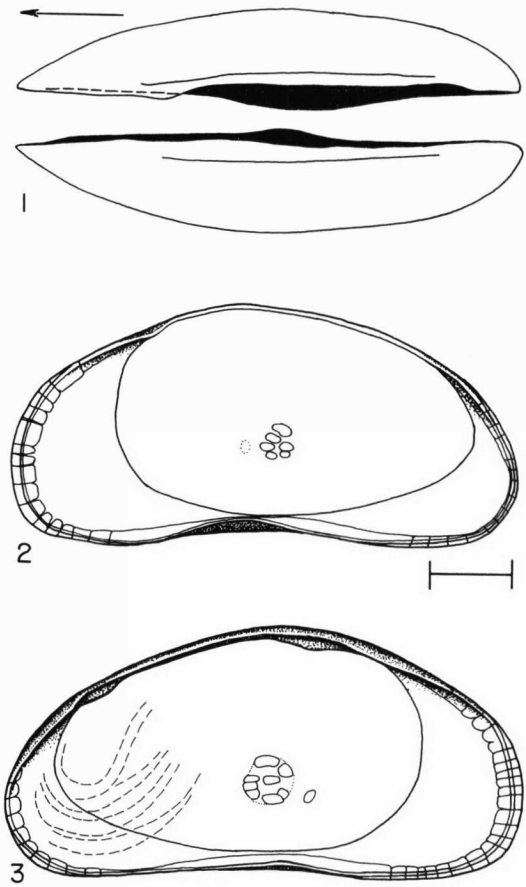


FIG. 28. Species DB.—*1*. Dorsal view of both valves.—*2*. Interior of right valve.—*3*. Interior of left valve showing soft remnants of testes between the inner and outer lamellae.

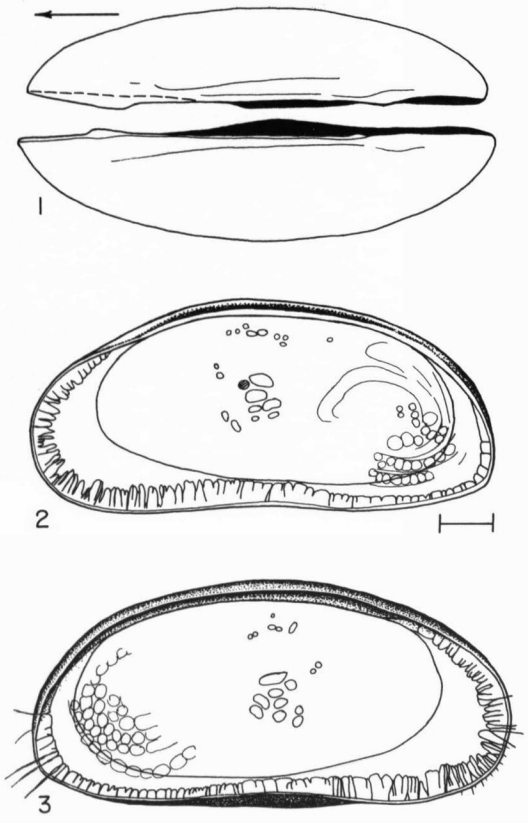


FIG. 29. Species DD.—*1*. Dorsal view of both valves.—*2*. Interior of right valve.—*3*. Interior of left valve.

Type.—Colorless adult male collected living from sta. 310 (Fig. 28). LV L, 0.61 mm.; H, 0.31 mm.; RV L, 0.60 mm.; H, 0.29 mm.

Habitat.—Colorful variant extremely abundant in washings of alga type BR growing on shoreline boulders at midtide level at loc. 4, also in washings of mud- and alga-encrusted mangrove pneumatophores at loc. 16. Colorless forms present in variety of environments: washings of alga A, of hermit crabs and shells, and sand among corals at loc. 1; carbonate sand from *Cymodocea* beds at locs. 3 and 11; algae and intertidal sand at loc. 6; fore-reef sand at loc. 13 and Pte. Tafondro; *Cymodocea*, shell accumulations on the lower beach at loc. 5; *Thallassia* at loc. 16; an alcyonarian at loc. 14.

Subfossil distribution.—Very numerous in a collection of small pelecypod shells and associated quartz sand washed up on the lower beach at loc. 5; also present in reef and fore-reef sands at loc. 1, 9, and 13; carbonate sands of the *Cymodocea* beds at locs. 3 and 11, intertidal sand at loc. 16.

Genus AGLAIELLA Daday, 1910

Species DD

Carapace smooth, moderately inflated, dorsal margin nearly horizontal, posterior end bluntly terminated. Zone of concrescence wide, crossed by numerous irregularly distributed radial pore canals and false radial pore canals, some branching; line of concrescence rather uneven. Zenckers organs of male bearing eight whorls of radiating spikes. Living specimens mottled brown, body and appendages yellow. Subfossil carapaces transparent or white.

Remarks—Considerable variation in length-height ratio not explained entirely by sexual dimorphism.

Type.—Large male collected living from sta. 341 (Fig. 29). LV L, 0.86 mm.; H, 0.41 mm.; RV L, 0.83 mm.; H, 0.39 mm.

Habitat.—Abundant on exposed surface of soft intertidal mud dotted with small crustacean burrows at loc. 4; common in intertidal muds and beach sands at locs. 5, 16, 17; also collected living in carbonate sands from loc. 3, 9, and soft clay at 10 m. depth in the Baie d'Ampasindava.

Subfossil distribution.—Abundant in calcareous, quartzose, and partly terrigenous nearshore and intertidal sands at locs. 5, 15, 16, 17, Pte. d'Andemby; intertidal mud at loc. 4; also present in carbonate and quartz-carbonate sands SW of Nosy Komba, south of Hellville, and in loc. 9; isolated specimens present in most samples of any sediment type.

Genus PARACYPRIS Sars, 1866

Species DJ

Carapace quite large, smooth; anterior margin broadly rounded, posterior end drawn out to a very acute ventral angle, highest point near anterior end; moderately inflated, thickest slightly anterior to midlength. Anterior duplicature very wide, with deep vestibule, irregularly lobate line of concrescence, bifurcating radial pore canals. Subfossil carapaces transparent, yellowish.

Type.—Intact subfossil carapace collected at sta. 237 (Fig. 30,*1*). RV L, 0.91 mm.; H, 0.35 mm.; W, 0.18 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Specimens found in intertidal quartz sand at loc. 5 and in intertidal mud composed mainly of vegetal and terrigenous detritus in the channel north of loc. 17.

Genus UNCERTAIN

Species DK

Carapace smooth, dorsal margin highly arched, greatest height just anterior to mid-length; compressed marginally, expanded medially, greatest thickness located somewhat above mid-height; ventral margin conspicuously indented. Radial

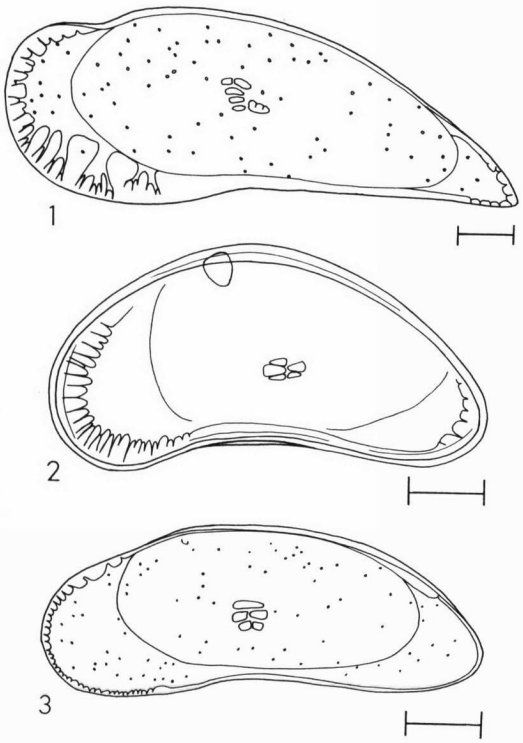


FIG. 30.—*1*. Species DJ, interior of right valve.—*2*. Species DK, left exterior view of whole specimen.—*3*. Species DH, interior of right valve.

pore canals apparently branching, muscle-scar pattern an aggregate of five scars. Carapace of living specimen yellowish and transparent with brown margins, body yellow, appendages dark yellow, eyes brown.

Type.—Adult female(?) collected living at sta. 158 (Fig. 30,*2*). L, 0.57 mm.; H, 0.29 mm.

Habitat.—Specimens found in washings of living corals from loc. 12.

Subfossil distribution.—The only subfossil specimen found in sand at low tide level at loc. 16.

Species DH

Carapace smooth, very compressed, elongate, dorsal margin nearly horizontal, anterior margin broadly rounded, posteroventral angle narrowly rounded, ventral margin slightly indented. Wide anterior and posterior vestibules, very narrow zone of concrescence with simple straight radial pore canals. Muscle-scar pattern aggregate of five scars. Carapace translucent white, body pale yellow.

Type.—Male collected living at sta. 476 (Fig. 30,*3*). LV L, 0.57 mm.; H, 0.23 mm.; RV L, 0.57 mm.; H, 0.22 mm.

Habitat.—Two living specimens found in carbonate sands of the *Cymodocea* beds of loc. 11 and among coral masses at loc. 1.

Species DF

Carapace extremely elongate, moderately inflated, dorsal margin horizontal, anterior and posterior margins broadly and equally rounded, ventral margin not sinuate. Anterior vestibule very deep, constricted dorsally by projecting lobe of zone of concrescence; posterior vestibule shallow; zone of concrescence moderately wide, with numerous short thin radial pore canals and false radial pore canals, some apparently branching; line of concrescence somewhat irregular. Hinge adont, muscle-scar pattern compact aggregate of cypridacean pattern. Ejaculatory ducts of male having six whorls of radiating spikes. Living specimen creamy yellow with light red streaks in the region of the eye and muscle scars.

Type.—Adult male specimen collected living at sta. 491 (Fig. 31). LV L, 0.87 mm.; H, 0.35 mm.; RV L, 0.86 mm.; H, 0.33 mm.

Habitat.—This form occurred living in carbonate and quartz-carbonate sands and sandy clays at locs. 13, Pte.

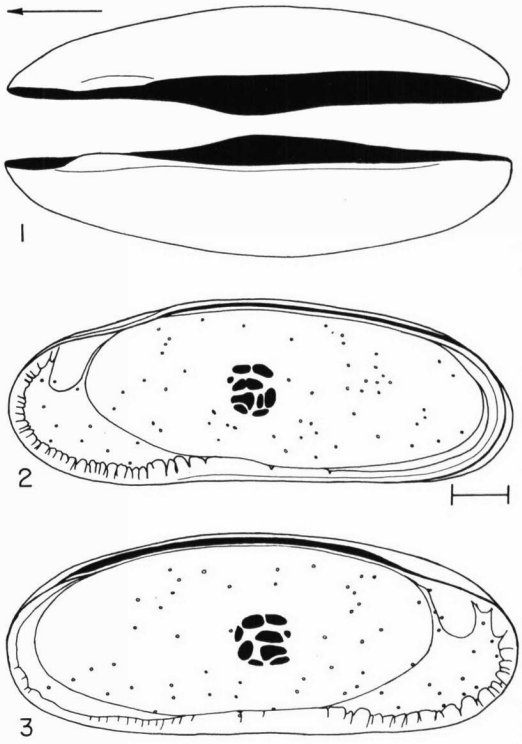


FIG. 31. Species DF.—*1*. Dorsal view of both valves.—*2*. Interior of right valve.—*3*. Interior of left valve.

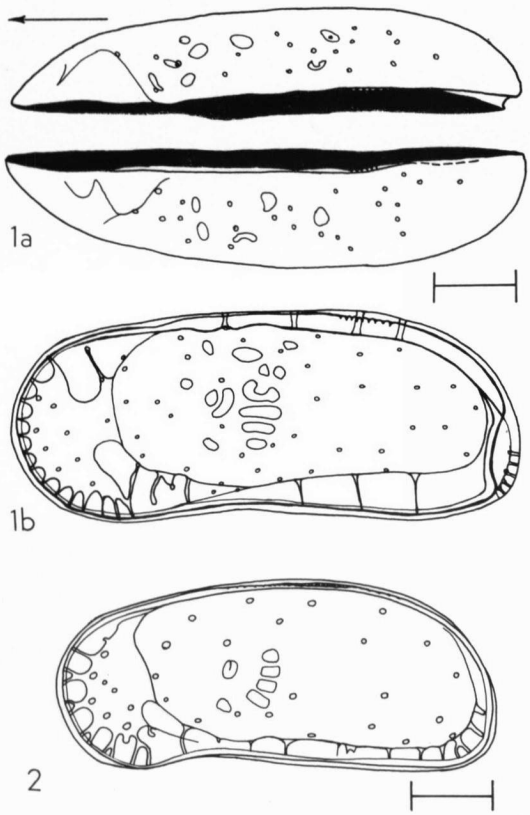


FIG. 32.—*1.* Species EA; *1a,* dorsal view of both valves; *1b,* interior of right valve.—*2.* Species EB, interior of right valve.

Tafondro, southeast of Nosy Komba, north of loc. 12, south of Hellville, Baie d'Ampasindava, and east of loc. 17.

Subfossil distribution.—Abundant in sediment at most of the localities cited above, occurring as well in carbonate sands and muds at locs. 9, 14, and west of Nosy Komba.

Family CYTHERIDEIDAE Sars, 1925

Subfamily KRITHINAE Mandelstam in Bubikan, 1958

Genus PARAKRITHELLA Hanai, 1961

Species EA

Carapace elongate, inflated, smooth; lacking posterior incision in dorsal view; anterior vestibule deep, zone of concrescence narrow and regularly lobate except for large dorsal and ventral lobes expanding into and constricting opening of vestibule, radial pore canals short and simple. Carapace of living specimen translucent, pale yellow, body yellow-brown.

Type.—Adult male specimen collected living from sta. 394 (Fig. 32,*1*). RV L, 0.62 mm.; H, 0.25 mm.; LV L, 0.61 mm.; H, 0.27 mm.

Habitat.—Recorded from carbonate and quartz-carbonate sands and sandy clays in loc. 9, east of Pte. Tafondro, south of Nosy Komba, and in the Baie d'Ampasindava.

Subfossil distribution.—Abundant at the stations mentioned above and at neighboring localities; present as well in intertidal and near-shore sands and offshore clays at many stations.

Species EB

Carapace small, elongate, smooth, lacking posterior incision in dorsal view. Hinge in left valve consists of narrow groove divided into anterior smooth and posterior crenulate sections; in right valve faintly crenulate bar is overlain medially by short crenulate depression. Radial pore canals short and thick, bifurcating, vestibule restricted ventrally by lobate extension of zone of concrescence; normal pore canals very large. Carapace of living specimen transparent, pale yellow, body black, appendages and genitalia dark yellow.

Type.—Adult male collected living at sta. 068 (Fig. 32,*2*). LV L, 0.55 mm.; H, 0.25 mm.; RV L, 0.54 mm.; H, 0.24 mm.

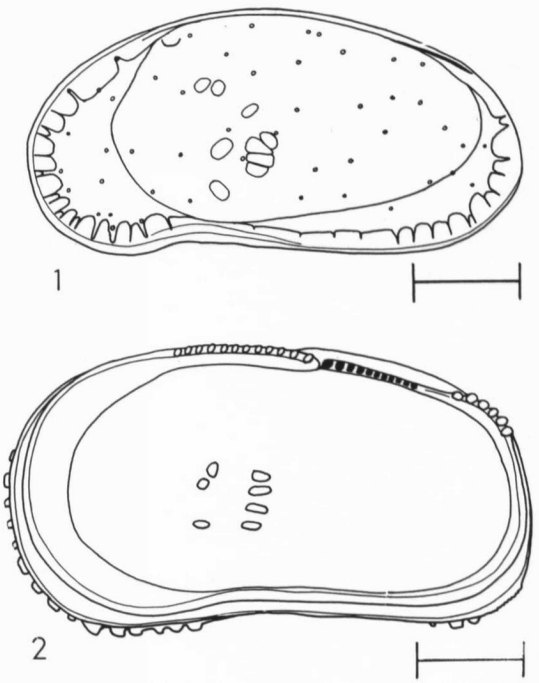


FIG. 33.—*1.* Species DG, interior of right valve.—*2.* Species NC, interior of right valve.

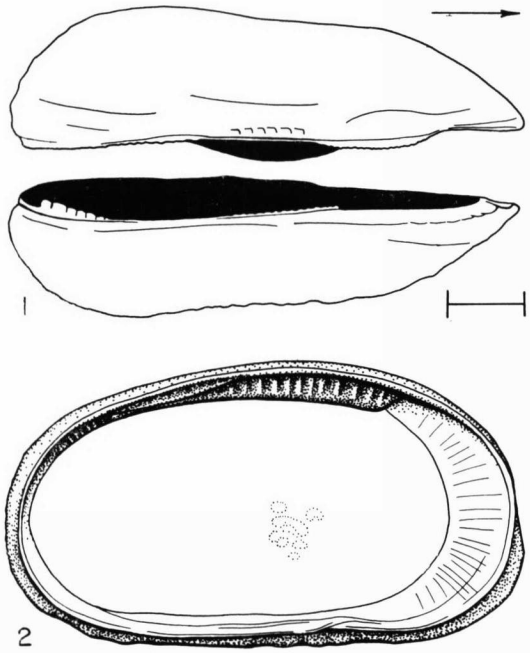


FIG. 34. Species NA.—*1*. Dorsal view of both valves.—*2*. Interior of left valve.

Habitat.—Found in washings of dead coral and shell fragment accumulations at loc. 11, an alga-encrusted living *Pinna* at loc. 5, and in intertidal quartz carbonate beach sand at loc. 5.

Subfamily UNCERTAIN

Genus UNCERTAIN

Species DG

Carapace smooth, moderately compressed, with greatest thickness at midlength and slightly below midheight. Anterior and posterior margins broadly rounded, ventral margin slightly sinuate, dorsal margin broadly arched. Hinge adont, radial pore canals thick and occasionally merging proximally, adductor muscle scars a vertical row of four fused scars. Living specimen yellow with mottled brown centrally.

Remarks.—Only muscle-scar pattern, not readily visible on living specimen, betrays cytheracean anatomy.

Type.—Female collected living at sta. 474 (Fig. 33,*1*). RV L, 0.45 mm.; H, 0.23 mm.

Habitat.—Three living specimens found in surface mud of mangrove-lined intertidal banks of loc. 8, fore-reef sand at loc. 13, sand among reef masses at loc. 1.

Species NC

Carapace small but robust, oblong in lateral view, nearly rectangular in dorsal view, margins denticulate. Exterior smooth with wide low ridge paralleling the anterior and ventral margins, somewhat removed from the margins, merging in posterior area with E-form posterior ridge, all bounded and emphasized by double row of large pits. Hinge antimerodont with prominent denticles.

Type.—Intact carapace collected subfossil at sta. 343 (Fig. 33,*2*). LV L, 0.51 mm.; H, 0.28 mm.; W, 0.15 mm.; RV L, 0.49 mm.; H, 0.27 mm.; W, 0.13 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Sparsely distributed in clays and muddy sands of Baie de Tsimipaika.

Species NA

Carapace robust, ovate in lateral view; exterior varying from nearly smooth to very coarsely punctate, margins tending to be denticulate. Hinge robust merodont, in left valve consisting of crenulate terminal sockets connected by narrow ridge with superposed shallow groove. Carapace of living animal translucent white, body brown and yellow, appendages dark yellow, eggs pale yellow.

Type.—Oviferous female collected living at sta. 492 (Fig. 34). Carapace very abundantly punctate. LV L, 0.64 mm.; H, 0.36 mm.; W, 0.22 mm.; RV L, 0.63 mm.; H, 0.33 mm.; W, 0.20 mm.

Habitat.—Soft clay at 15 to 20 m. in Baie d'Ampasindava; quartz-carbonate muddy sand south of Nosy Komba and in channel south of Nosy Faly; carbonate mud in loc. 9; carbonate fore-reef sand at loc. 2; algae and intertidal carbonate sand at loc. 16.

Subfossil distribution.—Present but not abundant in clays, sandy clays, and carbonate and quartzose sands from intertidal zone to 30 m., at many different localities.

Family HEMICYTHERIDAE Puri, 1953

Genus CAUDITES Coryell & Fields, 1937

Species HD

Very robust, reticulate carapace with prominent ridges and caudal extension. Hinge amphidont with narrow smooth median groove in right valve, posterior tooth bilobed, with anterior step, appearing trilobed. Inner lamella of wide vestibule fused to carapace forming pillar structures. Antennule five-segmented, exopodite of antenna as long as endopodite, thoracic legs with complex supporting structure present at knees. Carapace of living form translucent white, body bright red, appendages yellow, eyes red.

Remarks.—No males found among specimens.

Type.—Adult female collected living at sta. 446 (Fig. 35,*1*). LV L, 0.54 mm.; H, 0.30 mm.; RV L, 0.54 mm.; H, 0.29 mm.

Habitat.—Specimens of this species were recovered from washings of several types of calcareous algae, a solitary red ascidian, and dead coral fragment accumulations at locs. 3, 10, 11, 13; from alga-encrusted mangrove pneumatophores and noncalcareous algae at locs. 6, 13.

Subfossil distribution.—Single specimen found in carbonate sand near north shore of Nosy Komba.

Species HH

Carapace compressed, elongate, streamlined. Exterior smooth, with thickened smooth marginal and diagonal ridges. Inner lamella calcified and fused to outer lamella over most of internal surface. Hinge amphidont, median groove of right valve very narrow and smooth, posterior tooth with ventral indentation, anterior step. Adductor muscle scars with top three scars divided, three antennal scars. Antennule five-segmented, exopodite of antenna about two-thirds as long as endopodite, thoracic legs with complex supporting structure at knee. Carapace of living specimen translucent white, body brown and yellow, appendages yellow, eyes brown.

Remarks.—No males found among specimens.

Type.—Adult female collected living from sta. 521 (Fig. 35,*2*). L, 0.59 mm.; H, 0.31 mm., for both valves.

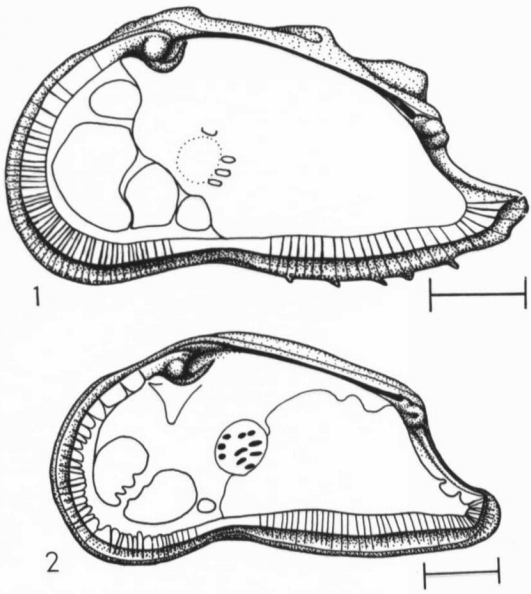


FIG. 35.—*1*. Species HD, interior of right valve.—*2*. Species HH, interior of right valve.

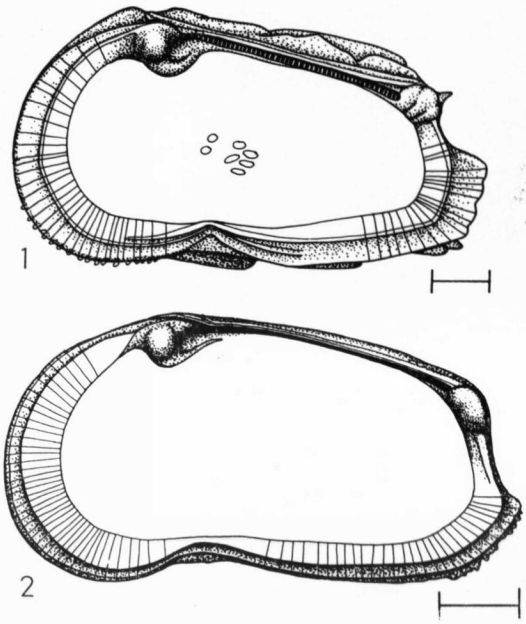


FIG. 36.—*1*. Species HP, interior of right valve.—*2*. Species HE, interior of right valve.

Habitat.—Specimens found in washings of three types of algae collected at loc. 10, associated with specimens of species HD.

Genus UNCERTAIN

Species HP

Carapace similar in general shape and ornamentation to species HA, differing from latter in following respects: posterior margin extended as distinct caudal process below mid-height; ridges of reticulate pattern much emphasized, with especially prominent anteromarginal, dorsal, median, and ventrolateral crestlike ridges; dorsal and median ridges connected in loop by short vertical posterior ridge, median ridge actually double ridge in area of subcentral tubercle; posterior hinge tooth in right valve trilobate. Antennule five-segmented, exopodite of antenna as long as endopodite, thoracic legs with complex supporting structure. Carapace of living specimen white, body and appendages yellow.

Remarks.—Continuous gradation may exist in expression of external sculpture from this very carinate and caudate species to more subquadrate and evenly reticulate species HA, as some apparently transitional specimens were found and as-

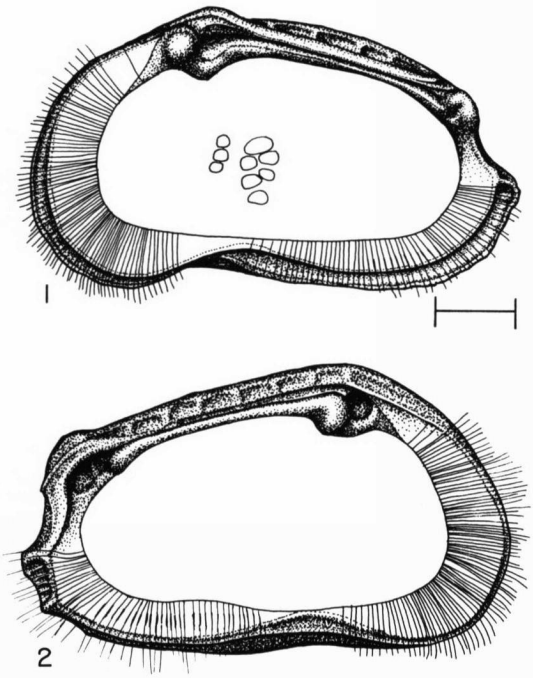


FIG. 37. Species HC.—*1*. Interior of right valve.—*2*. Interior of left valve.

signed to species HA. Only conspicuously tricarinate specimens were assigned to species HP.

Type.—Adult female collected living at sta. 289 (Fig. 36,*1*). RV L, 0.81 mm.; H, 0.46 mm.; W, 0.28 mm.; LV L, 0.81 mm.; H, 0.47 mm.; W, 0.24 mm.

Habitat.—Found in coarse sand among *Cymodocea* and dead coral fragments at loc. 3, in washings of dead coral fragments at loc. 6.

Subfossil distribution.—Sparsely distributed in carbonate beach and fore-reef sands and quartz-carbonate muddy sands offshore.

Species HE

Carapace subrectangular, much compressed, typically hemicytherid in shape. Exterior coarsely reticulate with closely spaced steep-walled pits, two posterodorsal and one ventrolateral nodose elevations, prominent eye tubercle. Hinge holamphidont, radial pore canals straight and closely spaced. Antennule five-segmented, exopodite of antenna as long as endopodite, thoracic legs with supporting structure at knees. Carapace of living form white with scattered black patches, body pale yellow, appendages and genitalia dark yellow.

Type.—Adult male specimen collected living from sta. 219 (Fig. 36,*2*). LV L, 0.64 mm.; H, 0.35 mm.; W, 0.18 mm.; RV L, 0.64 mm.; H, 0.35 mm.; W, 0.15 mm.

Habitat.—Abundant in washings of alga-encrusted *Tridacna* from loc. 14; also present in washings of several types of sponges, corals, and dead coral fragments from locs. 1, 2, 9, 12, 13, and in carbonate sand south of Nosy Komba.

Subfossil distribution.—Present but never very abundant in carbonate and quartz-carbonate sands at many localities.

Species HC

General form of carapace, hingement, muscle-scar pattern, and marginal features conformable to those established for *Mutilus*. Exterior coarsely reticulate with several ridges being especially prominent: anterodorsal ridge, continuous through ocular swelling with anteromarginal ridge continuous as ventral marginal ridge; alate ventrolateral ridge; dorsolateral ridge meeting posterior ridge in angulate projection; two staggered pairs of mediolateral horizontal ridges. Antennule five-segmented, exopodite of antenna as long as endopodite, thoracic legs with complex supporting structure at knees. Living specimen mottled black centrally with clear marginal areas; body and appendages pale yellow.

Type.—Adult male specimen collected living at sta. 060 (Fig. 37). LV L, 0.61 mm.; H, 0.34 mm.; W, 0.18 mm.; RV L, 0.61 mm.; H, 0.37 mm.; W, 0.15 mm.

Habitat.—Found indiscriminately and abundantly on algae of all kinds, grasses, sponges, living coral masses, alcyonarians, alga-encrusted reef-dwelling pelecypods, ac-

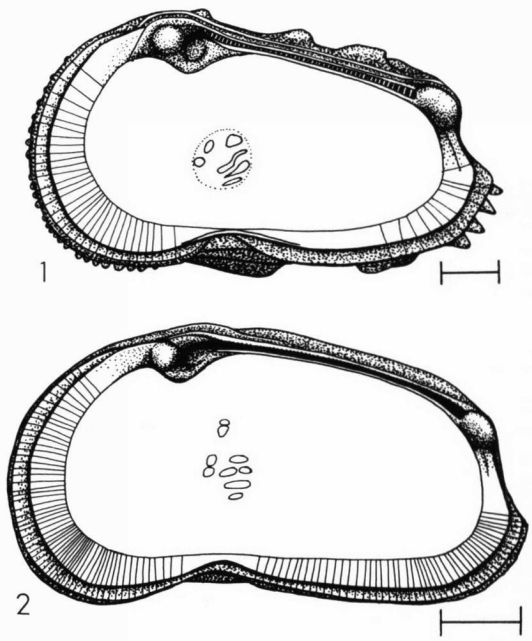


FIG. 38.—*1*. Species HA, interior of right valve.—*2*. Species HI, interior of right valve.

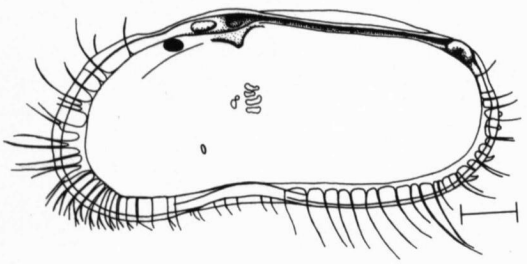


FIG. 39. Species KA, interior of right valve.

cumulations of dead coral and shell fragments, at all reef and shore collecting localities.

Subfossil distribution.—Present but never abundant in sands of all types, especially in carbonate sands associated with living corals.

Species HA

Carapace large, robust, subquadrate and much inflated, with flattened venter beneath alate ventrolateral swelling, well developed posterodorsal crest and subcentral elevation. Surface very coarsely reticulate with superimposed finer reticulate pattern of very tiny punctae. Hinge robust holamphidont, in right valve with crenulate median groove, smooth posterior tooth, shallow continuous groove overlying hinge dorsally. Antennule five-segmented, exopodite of antenna as long as endopodite, thoracic legs with complex supporting structure at knees. Carapace of living specimens opaque white, body and appendages yellow.

Type.—Adult male collected living from sta. 512 (Fig. 38,*1*). LV L, 0.82 mm.; H, 0.48 mm.; W, 0.26 mm.; RV L, 0.82 mm.; H, 0.47 mm.; W, 0.25 mm.

Habitat.—Found in many varieties of algae and grasses and on dead coral fragment accumulations at nearly all shore collecting localities.

Subfossil distribution.—Widely distributed in sediments of many types, particularly abundant in carbonate and quartz-carbonate sands and sandy muds near areas of living coral, especially north of loc. 12, south of Hellville, east of Nosy Komba, loc. 14, and Passe de Nosy Vorona.

Species HI

Carapace typically hemicytherid in shape, compressed, coarsely reticulate with a regular pattern of uniformly elevated longitudinal ribs and prominent anteromarginal ridge, but without alate ventrolateral or posterodorsal prominences. Hinge holamphidont, radial pore canals very numerous and straight. Antennule five-segmented, exopodite of antenna as long as endopodite, thoracic legs with complex supporting structure at knees. Carapace of living specimen yellowish white, body and appendages yellow.

Type.—Adult male specimen collected living at sta. 527 (Fig. 38,*2*). LV L, 0.65 mm.; H, 0.35 mm.; W, 0.18 mm.; RV L, 0.65 mm.; H, 0.36 mm.; W, 0.16 mm.

Habitat.—Found in washings of alga type BH and several other types of algae and of dead coral fragments, from all shore collecting localities, mid- to low-tide level.

Subfossil distribution.—Present but sparse in carbonate sands from most localities, also reported from quartz beach sand at loc. 5 and terrigenous soft intertidal mud at loc. 4.

Species KA

Carapace oblong in lateral and dorsal view, much inflated; exterior with striate pattern of low longitudinal ridges separated by punctate grooves, two anteromarginal rows of large deep pits. Hinge elongate but strongly amphidont, toothlike projection present below anterior hinge element; radial pore canals thick, fairly numerous, widening proximally, in anterior region merging with adjacent canals to produce a lobate line of concrescence; small posterior vestibule present. Antennules six-segmented, exopodite of antenna as long as endopodite, thoracic legs with complex supporting structures at knees. Carapace of living specimens translucent white, body light bluish green. Subfossil carapaces translucent white.

Type.—Adult male from sta. 239, collected living (Fig. 39). RV L, 0.77 mm.; H, 0.26 mm.; W, 0.21 mm.

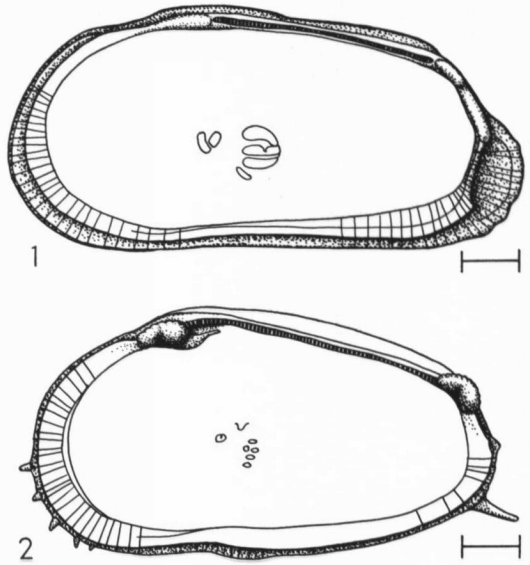


FIG. 40.—*1*. Species HK, interior of right valve.—*2*. Species HQ, interior of right valve.

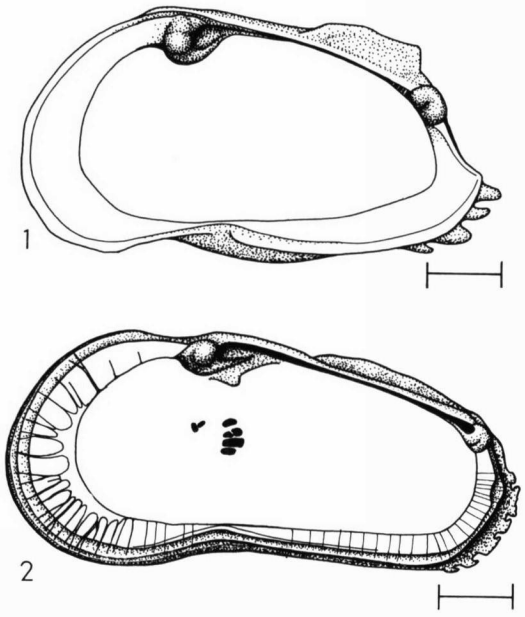


FIG. 41.—*1*. Species HL, interior of right valve.—*2*. Species HM, interior of right valve.

Habitat.—Found in abundance in intertidal quartz and carbonate beach sand at locs. 5, 16, 17; also reported in certain algae on these beaches.

Subfossil distribution.—Abundant in intertidal and nearshore sands at locs. 5 and 16, also in carbonate sands at other intertidal and nearshore localities.

Family HEMICYTHERIDAE Puri, 1953 or TRACHYLEBERIDIDAE Sylvester-Bradley, 1948

Genus UNCERTAIN

Species HK

Carapace large, moderately inflated; coarsely reticulate with especially prominent continuous longitudinal ridges and grooves; posteroventral margin extended in caudate fashion. Hinge weakly amphidont with crenulate median element; radial pore canals numerous and straight.

Type.—RV collected subfossil from sta. 327 (Fig. 40,*1*). L, 0.86 mm.; H, 0.43 mm.; W, 0.20 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Specimens found in intertidal muddy sand among mangrove pneumatophores at loc. 16.

Species HQ

Carapace elongate-ovate in lateral view, somewhat inflated medially but without abrupt posterior compression or alate development. Surface with reticulate ornament of longitudinal rows of large pits, especially prominent on posterior half of carapace. Few anteromarginal denticles, one large posteromarginal spine, no spines on the ventrolateral surface. Hinge robust amphidont, in right valve with prominent anterior and posterior bilobed teeth finely crenulate on dorsal sides, narrow crenulate median groove curving around ovate, shallow anteromedian socket.

Type.—Right valve collected subfossil from sta. 354 (Fig. 40,*2*). L, 0.84 mm.; H, 0.43 mm.; W, 0.29 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Intertidal quartz sand at loc. 5, quartz carbonate sand in channel south of Nosy Faly, carbonate sand and soft clay at depths of 10 to 25 m. in Baie de Tsimipaika.

Species HL

Carapace similar in general shape and ornamentation to that of species HA, differing in following respects: smaller in size, being about the same size as last instar of species HA; posterior margin extended in caudate fashion and terminated as four large spines; ventrolateral ala more prominent and emphasized marginally by pair of irregular ridges; posterodorsal crest projecting as angulate loop; pair of short ridges surmount the subcentral tubercle; hinge narrower, lacking crenulations in the median element, the posterior hinge tooth in right valve more distinctly grooved ventrally. Carapace also very similar to that of species HP, from which it differs in its smaller size, shallower pits in the general reticulate pattern, less prominent and unevenly elevated main ridges, absence of continuous median ridge, and less robust hinge, lacking crenulations on median element and with posterior tooth reniform rather than trilobate.

Type.—Intact carapace collected subfossil at sta. 466 (Fig. 41,*1*). LV L, 0.64 mm.; H, 0.35 mm.; W, 0.24 mm.; RV L, 0.63 mm.; H, 0.34 mm.; W, 0.21 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Sparse but present in most calcareous reef sands, occasionally found in quartz-carbonate sands and sandy muds.

Species HM

Carapace subquadrangular in lateral outline, anterior margin broadly rounded, ventral margin bluntly truncate and coarsely denticulate, dorsal margin sloping posteriorly from highest point near anterior. Domicilium moderately inflated, greatest thickness near midlength, abruptly compressed posteroventrally. Surface coarsely reticulate, with deep polygonal pits bounded by thin

ridges in diagonal-longitudinal rows. Hinge holamphidont with bilobate posterior tooth in right valve; branching radial pore canals anteriorly, opening into shallow vestibule. Adductor muscle scars vertical row of four scars, the second scar from top divided, antennal scars V-form. Carapace of preserved specimen yellowish white, body colorless.

Remarks.—Two living specimens cited are juveniles, not yet dissected; hence family affinity uncertain.

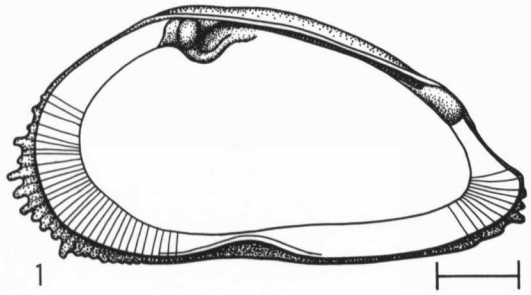
Type.—Intact carapace, probably of male, found subfossil at sta. 395 (Fig. 41,2). LV L, 0.68 mm.; H, 0.33 mm.; W, 0.14 mm.; RV L, 0.68 mm.; H, 0.32 mm.; W, 0.19 mm.

Habitat.—Juveniles found in washings of *Syringodium* from loc. 5 and of alga BO attached on boulders at low tide level at loc. 2.

Subfossil distribution.—Present but never abundant in intertidal and fore-reef carbonate sands, intertidal and offshore quartzose and carbonate sands and sandy muds.

Species HN

Carapace similar in shape to that of species HJ, differing in following respects: smaller size, less inflation, ornament evenly reticulate rather than longitudinal ridges and grooves, with deeply incised pits. Nature of reticulate ornament very much like that of species HB, but does not display ventrolateral alate development of latter species and has holamphidont hingement. It differs from species HF in its ovate lateral outline, greater inflation, and more regularly reticulate surface sculpture.



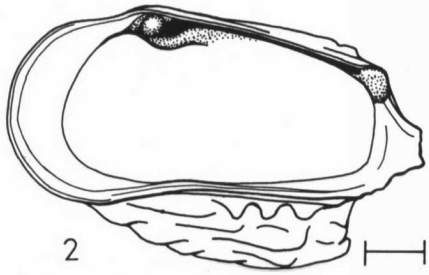


FIG. 42.—*1.* Species HN, interior of right valve.—*2.* Species HO, interior of right valve.

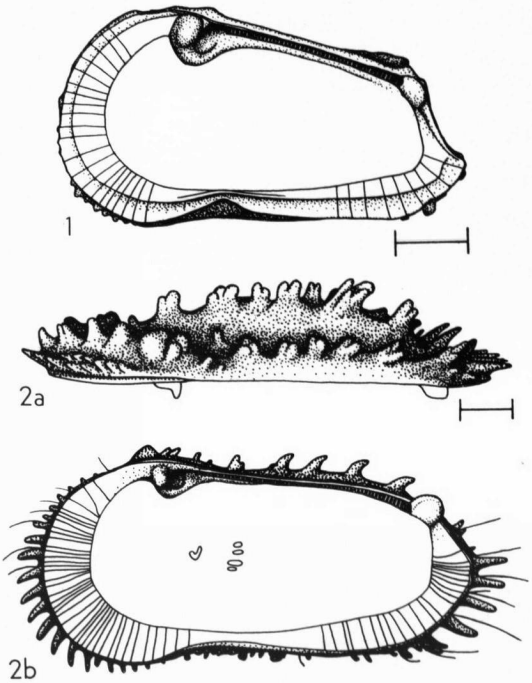


FIG. 43.—*1.* Species TB, interior of left valve.—*2.* Species TA; *2a,* dorsal view of right valve; *2b,* interior of right valve.

Type.—Intact carapace collected subfossil from sta. 491 (Fig. 42,*1*). LV L, 0.63 mm.; H, 0.34 mm.; RV L, 0.62 mm.; H, 0.33 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Specimens found in single sample of soft clay with oyster fragments in Baie d'Ampasindava.

Species HO

Carapace similar in shape to that of species HA, but subtriangular in cross section, with subdued dorsolateral crest, prominent ventrolateral alate expansion, flattened venter, lacking any anteromarginal or median ridges or subcentral tubercle. Surface evenly reticulate with regular pattern of deeply incised pits. Posterior hinge tooth of right valve smooth.

Type.—RV collected subfossil from sta. 070 (Fig. 42,2). L, 0.70 mm.; H, 0.41 mm.; W, 0.22 mm.

Habitat.—No living specimens found.

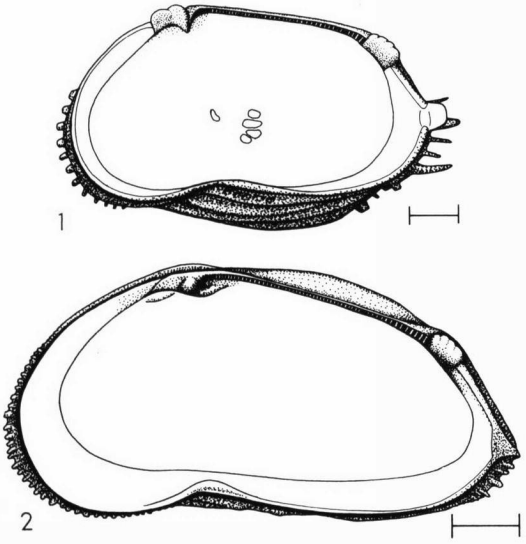


FIG. 44.—*1*. Species HB, interior of right valve.—*2*. Species HF, interior of right valve.

Subfossil distribution.—Found in four samples of carbonate sand at locs. 9, 10, 11, and 16.

Species TB

Carapace very robust, small, compressed, trachyleberid in shape; exterior with reticulate pattern of deeply excavated polygonal pits; conspicuous subcentral tubercle, ocular and posterodorsal nodes, alate ventrolateral ridge; margins spinose.

Type.—Intact carapace collected subfossil at sta. 070 (Fig. 43,*1*). LV L, 0.57 mm.; H, 0.32 mm.; W, 0.18 mm.; RV L, 0.57 mm.; H, 0.31 mm.; W, 0.17 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Subfossil specimens found in carbonate sand from 5 m. at loc. 11, and from exposed surface mud among mangroves at loc. 16.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948

Genus UNCERTAIN

Species TA

Carapace of adult compressed, robust, typically trachyleberid in outline; smooth except for circum-marginal, median, and ventrolateral rows of thick polydactyl nodes and spines, marginal spines being very long and curved. Immature specimens possess only single ventrolateral row of single curved tubular spines; marginal spines relatively much longer and more curved than those of adult. Hinge robust holamphidont with secondary crenulation of median element; muscle scar pattern consists of vertical row of four scars and V-shaped anterior scar. Antennule composed of six segments, exopodite of antenna about half as long as endopodite, thoracic legs without any complex chitinous supporting structure at knee. Carapace of living specimen transparent yellowish white, body and appendages yellow.

Type.—Adult male collected living at sta. 232 (Fig. 43,*2*). RV L (including spines), 0.92 mm.; H, 0.43 mm.

Habitat.—Form occurred living in muddy sands from loc. 17 and southeast of Nosy Komba, at depths of 5 to 15 m.

Subfossil distribution.—Abundant constituent of carbonate and quartz-carbonate muddy sands and clays in depths of 10 to 15 m., present in lesser abundance in many carbonate and quartz intertidal and reef sands.

Species HB

Carapace much inflated, flattened ventrally, domicilium produced ventrolaterally in alate fashion, compressed posteriorly. Surface bearing regular reticulate pattern of concentrically aligned, deeply incised polygonal pits; margins and alae with spines; lacking any expression of ocular swelling, subcentral tubercle, or other ridge or node development. Hinge amphidont, median and posterior elements faintly crenulate. Antennule six-segmented, exopodite of antenna one-third as long as endopodite, thoracic legs without complex supporting structure. Carapace of living specimen white, body brown, appendages yellow.

Remarks.—No male specimens found living, although some dimorphism appears among subfossil carapaces.

Type.—Female collected living from sta. 083 (Fig. 44,*1*). Narrow calcified inner lamella usual in this species.

Habitat.—Living specimens found in washings of alga type A and associated beach sand from loc. 5, alga type A from loc. 7, and sand among coral masses at loc. 12.

Subfossil distribution.—Extremely widespread, occurring in low frequencies in sediments of all types at most localities; especially abundant in carbonate and quartz-carbonate sands and muddy sands at loc. 9, south of Hellville, north of loc. 12, east of Pte. Tafondro, west and east of Nosy Komba, and in clays west of Pte. d'Andemby and in the Baie d'Ampasindava.

Species HF

Carapace very large and robust; exterior very coarsely sculptured in irregularly rugose pattern of thick curved ridges and deep fossae; margins denticulate. Hinge weakly hemiamphidont with crenulate median element; radial pore canals simple and quite numerous. Carapace of living speci-

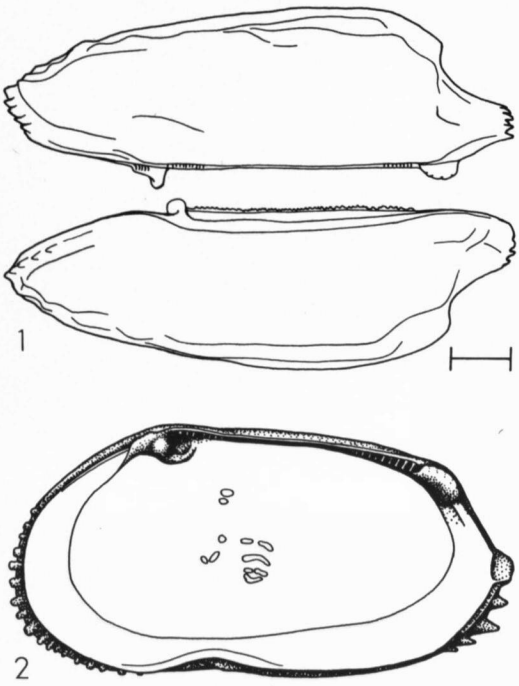


FIG. 45. Species HG.—*1*. Dorsal view of separated valves, slightly tilted.—*2*. Interior of right valve.

men yellowish white, body and appendages dark yellow.

Type.—Adult male collected living at sta. 082 (Fig. 44,*2*). L, 0.76 mm.; H, 0.38 mm.; W, 0.21 mm. for both valves.

Habitat.—Found living in carbonate sand at locs. 9, 13; on *Cymodocea*, alga type A and associated sand at loc. 5; alga type BR on shoreline boulders at mid-tide level at loc. 4; and in quartz carbonate sand southeast of Nosy Komba.

Subfossil distribution.—Present in carbonate and quartz-carbonate sands at all localities, especially abundant in intertidal sand at locs. 5, 16, 17 and in quartz sand at 12 m. west of Nosy Komba.

Species HG

Carapace robust, inflated, smooth except for thin horizontal ribs on posteroventral surface, compressed posteriorly, margins spinose. Hinge holamphidont with distinctly denticulate median elements, radial pore canals simple, straight, and fairly numerous. Antennule six-segmented, length of exopodite of antenna two-thirds that of endopodite, thoracic legs without complicated chitinous supporting structure at knees.

Type.—Adult female collected living from sta. 083 (Fig. 45). LV L, 0.83 mm.; H, 0.42 mm.; W, 0.22 mm.; RV L, 0.82 mm.; H, 0.42 mm.; W, 0.25 mm.

Habitat.—A single specimen was found living in quartz sand near low tide level on the beach at loc. 5.

Subfossil distribution.—Common in quartzose beach sand at locs. 5 and 15, in carbonate beach sand at loc. 16, carbonate sand in locs. 1, 9, and 14.

Species HJ

Carapace very large, subpyriform, much inflated. Exterior with concentric pattern of curved longitudinal ridges separated by subreticulate grooves, margins denticulate. Hinge holamphidont with narrow crenulate median groove and somewhat irregular posterior tooth in right valve. Radial pore canals straight, fairly numerous. Antennule six-segmented, exopodite of antenna nearly as long as endopodite, knees of thoracic legs without complex supporting structure. Carapace of living specimen yellowish white, body yellow with red-brown patches dorsally, appendages yellow.

Type.—Adult male collected living at sta. 345 (Fig. 46,*1*). RV L, 1.05 mm.; H, 0.51 mm.; W, 0.36 mm.; LV L, 1.04 mm.; H, 0.53 mm.; W, 0.32 mm.

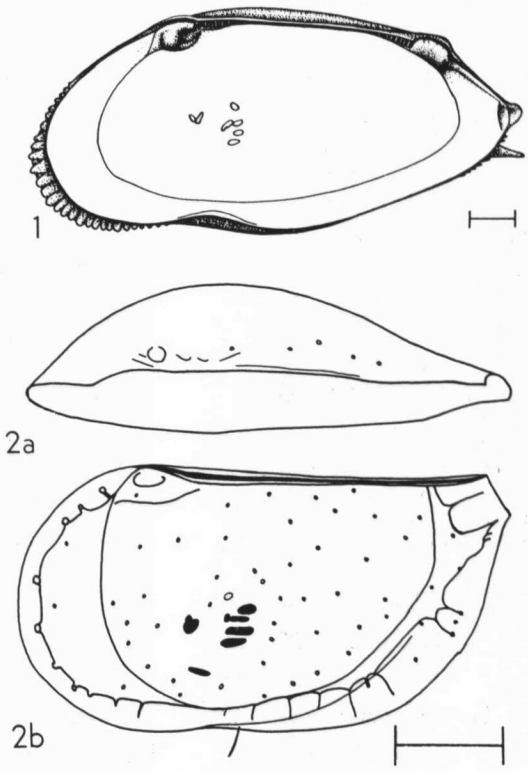


FIG. 46.—1. Species HJ, interior of right valve.—*2*. Species IA; *2a*, dorsal view of right valve, slightly tilted; *2b*, interior view of right valve.

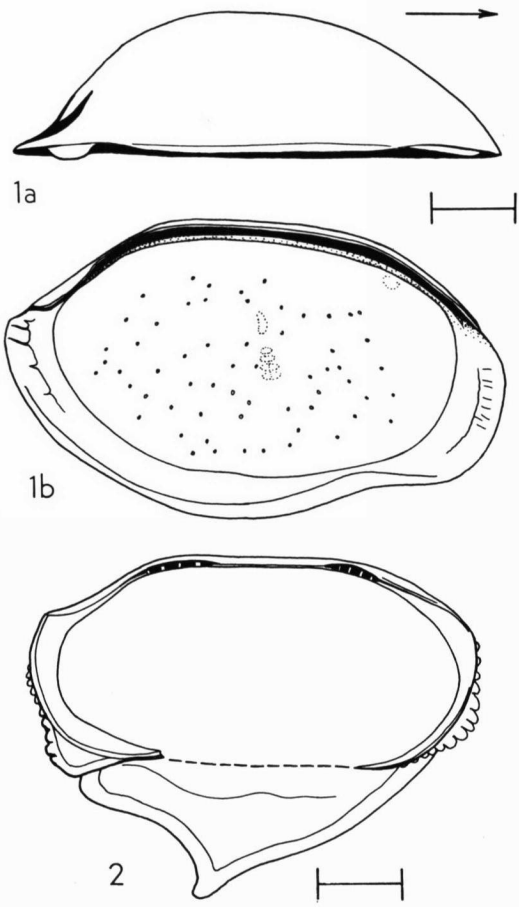


FIG. 47.—*1*. Species RB; *1a*, dorsal view of left valve; *1b*, interior of left valve.—*2*. Species RD; interior of left valve, ventral margin broken away.

Habitat.—Common in quartz carbonate muddy sands at depths of 10 to 15 m. at several stations, carbonate reef sands at loc. 9 and 13; one specimen was reported from washings of a green sponge at loc. 1.

Subfossil distribution.—Very abundant in most sediments where found living, abundantly distributed in coarse carbonate sands and quartz-carbonate muddy sands from many localities, especially near Nosy Komba; less numerous but present in finer sediments at several stations.

Family BYTHOCYTHERIDAE Sars, 1926

Genus PSEUDOCYTHERE Sars, 1866

Species IA

Carapace rather more inflated than usual for this genus, zone of concrescence narrower, radial pore canals few and short, apparently only four adductor muscle scars. Carapace of preserved specimen entirely white, body faintly yellowish.

Type.—Male specimen collected living from sta. 196 (Fig. 46,*2*). LV possesses posteroventral marginal projection typical of most forms of *Pseudocythere*. RV L, 0.43 mm.; H, 0.24 mm.

Habitat.—Specimens collected from washings of alga type A at loc. 1 and a solitary red ascidian at loc. 13.

Subfossil distribution.—The only subfossil occurrence of this form was in quartz-carbonate muddy sand south of Nosy Komba.

Genus BYTHOCYTHERE Sars, 1866

Species RB

Carapace small, rounded subrhomboidal in lateral view, much inflated, subalate with flattened venter, posteriorly compressed with caudal process. Surface smooth except for few small pits in longitudinal rows on dorsal and ventral surfaces of ventral swelling. Hinge simple lophodont. Carapace translucent white, body pale yellow or colorless.

Remarks.—Although dimorphism is evident among subfossil carapaces collected, no male specimens found living.

Type.—Adult female collected living at sta. 474 (Fig. 47,*1*). LV L, 0.57 mm.; H, 0.35 mm.

Habitat.—Living specimens collected from washings of alga type A from loc. 1, and from carbonate fore-reef sand at loc. 13.

Subfossil distribution.—Most numerous in two samples of calcareous sandy muds from north of loc. 12 at 24 m. and east of Nosy Komba at 10 m.; present but never abundant in carbonate fore-reef sands, sandy muds, and clays from many localities.

Genus MONOCERATINA Roth, 1928

Species RD

Carapace in lateral outline subrectangular with beveled angles, anterior and posterior margins denticulate; with ventrally directed thin pointed ala; without sulcus; surface with reticulate ornament of closely spaced small shallow pits. Hinge of left valve lophodont with shallow faintly crenulate sockets, smooth median ridge.

Type.—LV collected subfossil at sta. 070 (Fig. 47,*2*). LV L, 0.54 mm.; H (including ala), 0.37 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Single specimen found in sand with *Thallassia* at about 5 m. at loc. 11.

Genus UNCERTAIN

Species IB

Carapace robust, deeply sulcate, domicilium compressed, with very extended thick rugose ala;

thick nodose crest along straight dorsal margin, no caudal process. Hinge lophodont with crenulate terminal elements.

Type.—LV collected subfossil from sta. 491 (Fig. 48,*1*). LV L, 0.53 mm.; H (including ala), 0.29 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Specimens found in soft clay with oyster fragments at 10 m. in the Baie d'Ampasindava.

Family LEPTOCYTHERIDAE Hanai, 1957

Genus CALLISTOCYTHERE Ruggieri, 1953

Species JA

Carapace very small, compressed, surface coarsely sculptured with irregular ridges and pits of varying sizes. Zone of concrescence very wide, radial pore canals apparently fairly sparse, curved, and branching. Hinge very narrow, in right valve consisting of shallow finely crenulate anterior socket, curved crenulate posterior socket, joined by narrow curving ridge that is serrate at anterior end. Carapace and body bright yellow.

Type.—Adult male specimen collected living from sta. 324A (Fig. 48,*2*). LV L, 0.36 mm.; H, 0.19 mm.; RV L, 0.36 mm.; H, 0.19 mm.

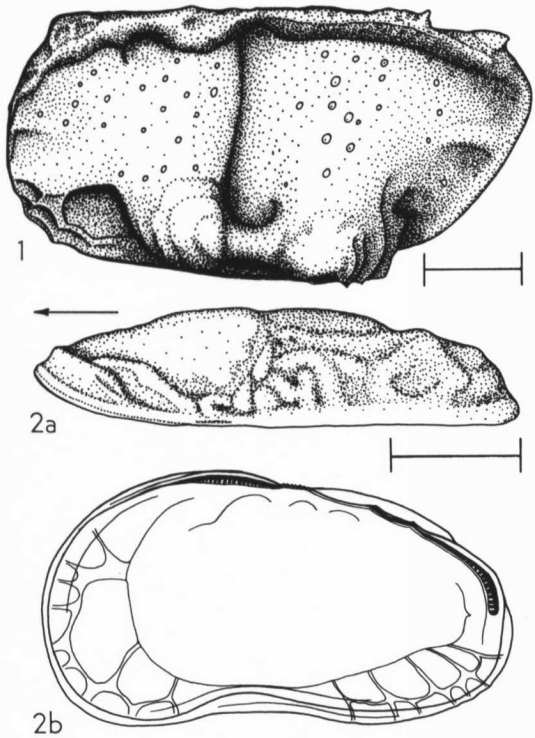


FIG. 48.—*1.* Species IB, exterior of left valve.—*2.* Species JA; *2a,* dorsal view of right valve; *2b,* interior of right valve.

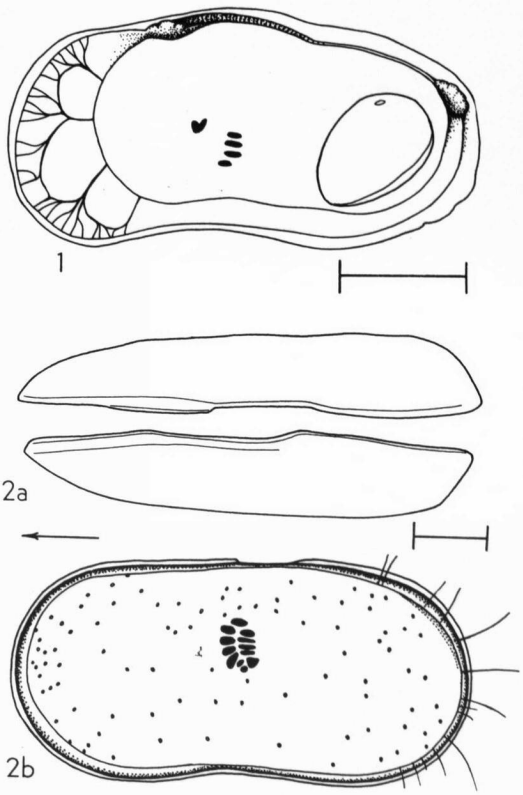


FIG. 49.—*1.* Species JB, interior of right valve, containing carapace of small instar in posterior cavity.—*2.* Species LA; *2a,* dorsal view of both valves; *2b,* interior of right valve.

Habitat.—Washings of sponges and alga type X at the Centre, a solitary red ascidian at loc. 13, exposed mangrove pneumatophores and surrounding mud at loc. 16, carbonate beach sand at loc. 1, quartzose beach sand at loc. 5.

Subfossil distribution.—No subfossil specimens found.

Genus LEPTOCYTHERE Sars, 1925

Species JB

Carapace moderately compressed, bearing an irregularly reticulate pattern of small pits, greatest thickness just before posterior end. Radial pore canals complexly branching. Carapace of living specimen transparent yellowish, body reddish brown, appendages yellow, eye brown, instar yellowish white.

Type.—Adult female collected living at sta. 225 (Fig. 49,*1*). Of two instars in posterior cavity of carapace, the more mature one is figured. RV L, 0.37 mm.; H, 0.19 mm.

Habitat.—Solitary red ascidian and alga type V at loc.

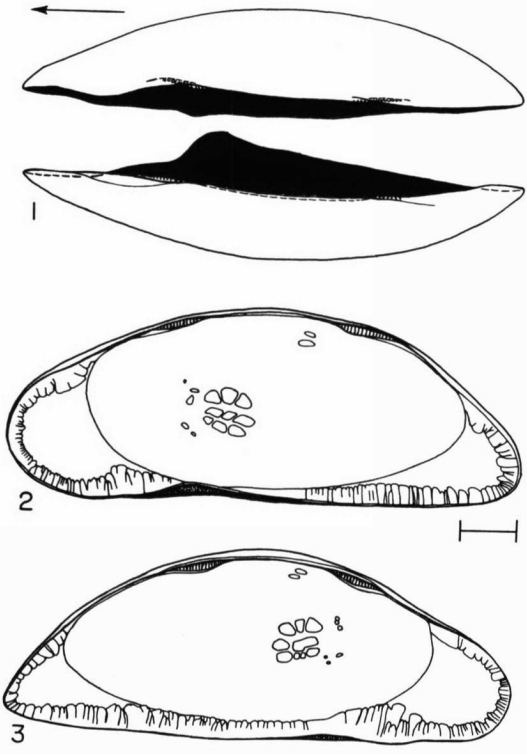


FIG. 50. Species MA.—*1*. Dorsal view of both valves.—*2*. Interior of right valve.—*3*. Interior of left valve.

13, quartz-carbonate beach sand at loc. 5, intertidal mud at loc. 16.

Subfossil distribution.—No subfossil specimens found.

Family CYTHERELLIDAE Sars, 1866

Genus CYTHERELLA Jones, 1849

Species LA

Carapace smooth, very compressed, greatest thickness immediately before posterior end, female carapace slightly more inflated and angulate posteriorly than that of male. Small pits of variable abundance may be present in broad band paralleling anterior, ventral, and posterior margins. Carapace of living form translucent white, body pale yellow.

Remarks.—Certain abundantly pitted specimens take on cytherelloidean appearance, but because of highly variable expression of pitting were not distinguished as separate species.

Type.—Adult male collected living from sta. 492 (Fig. 49,*2*). LV L, 0.58 mm.; H, 0.28 mm.; RV L, 0.59 mm.; H, 0.29 mm.

Habitat.—Specimens found living in soft clay at 15 m. west of Pte. d'Andemby, quartz-carbonate muddy sand south of Nosy Komba at 11 m., carbonate mud in loc. 9, soft clay at 15 m. in the Baie d'Ampasindava.

Subfossil distribution.—Widely distributed but never abundant in clays and sandy muds; rare in carbonate sands.

Family MACROCYPRIDIDAE G. W. Müller, 1912

Genus MACROCYPRINA Triebel, 1960

Species MA

Very large, elongate form with gently arched dorsal margin and narrowly rounded posteroventral angle. Zone of concrescence moderately wide, crossed by numerous straight and apparently branching radial pore canals and false radial pore canals. Five-part hinge, muscle scar pattern, Zenckers organ, and appendage morphology typical for genus. Carapace of living specimen translucent white, body deep yellow with few small brown streaks, appendages brown distally. Subfossil specimens usually retain some trace of pattern as irregular white and transparent areas.

Type.—Adult male collected living at sta. 212 (Fig. 50). LV L, 1.44 mm.; H, 0.56 mm.; RV L, 1.44 mm.; H, 0.57 mm.

Habitat.—Found commonly in washings of diverse algae, *Tridacna*, solitary red ascidian, and especially of dead coral fragments at locs. 3, 5, 9, 10, 11, 12, and 14; in carbonate sand at loc. 13 and west of Pte. d'Andemby.

Subfossil distribution.—Present in moderate abundance

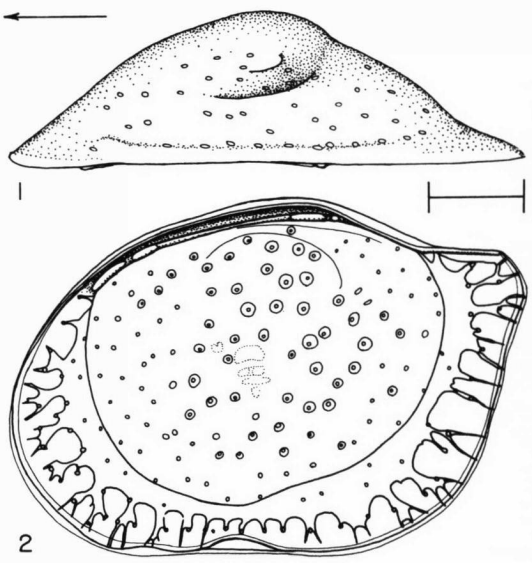


FIG. 51. Species OA.—*1*. Dorsal view of right valve.—*2*. Interior of right valve.

in quartz carbonate sands and sandy muds in 15 to 25 m. south of Nosy Bé, soft clay at 15 m. in the Baie d'Ampasindava; sparsely distributed in carbonate and quartz-carbonate sands and sandy clays at many intertidal and offshore localities.

Family LOXOCONCHIDAE Sars, 1925

Genus LOXOCONCHELLA Triebel, 1954

Species OA

Carapace subrhomboidal in lateral outline, with distinct caudal process at posterodorsal corner; very much inflated in dorsal view, greatest thickness at midlength; dorsolateral surface produced into subconical "horn" medially. Surface smooth except for numerous pits that are widened openings for funnel-shaped normal pore canals. Hinge pattern gongylodont, elements narrow but distinctly developed, not crenulate. Duplicature very wide, vestibule wide and continuous; line of concrescence extremely lobate, radial pore canals of varying length and thickness, merging proximally to form branching clusters of two to four canals. Carapace of living specimen transparent, yellowish; body yellow with reddish brown spots, appendages yellow. Subfossil carapace transparent and colorless.

Type.—Male collected living from sta. 286 (Fig. 51). RV L, 0.51 mm.; H, 0.37 mm.

Habitat.—Many types of algae, especially *Padina*, algae types X and W; *Cymodocea, Thallassia*; dead coral fragments; at loc. 6, Antsakoabe, the Centre, and several other shore collecting localities.

Subfossil distribution.—Present but sparse in carbonate intertidal, reef, and fore-reef sands.

Genus LOXOCORNICULUM Benson & Coleman, 1963

Species OB

Carapace strongly reticulate, posterodorsal and ventrolateral nodose elevations well developed, often with curved ventrolateral ridge distinguished as well; inflated medially, compressed posteriorly, distinct caudal process. Hinge well developed gongylodont with denticulate median elements. Carapace of living specimen transparent yellowish, body yellow to yellow-brown, appendages yellow.

Remarks.—Specimens included in this group display considerable variability in degree of expression of reticulate ornament and nodes. Extreme heterogeneity indicates that two or more species are combined here; however, no attempt was made to distinguish these variants as distinct categories. Certain specimens entirely without elevated nodes or ridges and having more subdued regularly reticulate ornament also included here, on basis of lateral and dorsal outlines and presence of caudal process.

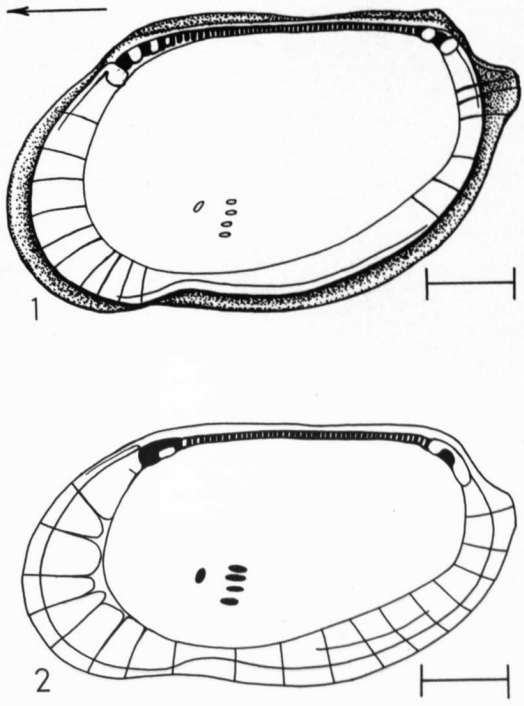


FIG. 52.—*1*. Species OB, interior of right valve.—*2*. Species OC, interior of right valve.

Type.—Adult male collected living at sta. 212 (Fig. 52,*1*). Strongly reticulate, with well developed dorsal and ventrolateral nodes. LV L, 0.59 mm.; H, 0.36 mm.; W, 0.20 mm.; RV L, 0.60 mm.; H, 0.36 mm.; W, 0.20 mm.

Habitat.—Extremely abundant and widely distributed among all types of algae and grasses and on accumulations of dead coral fragments; less common on sponges and in beach and reef sands.

Subfossil distribution.—Common in intertidal carbonate and quartzose sands, carbonate reef and fore-reef sands; scattered occurrences in carbonate and quartz-carbonate sands, sandy muds, and clays from offshore localities.

Genus LOXOCONCHA Sars, 1866

Species OC

Carapace much inflated, subrhomboidal in lateral view, subelliptical in dorsal view, without any posterodorsal nodes, alate expansion, or caudal process; males somewhat compressed posteroventrally. Surface with strongly reticulate pattern

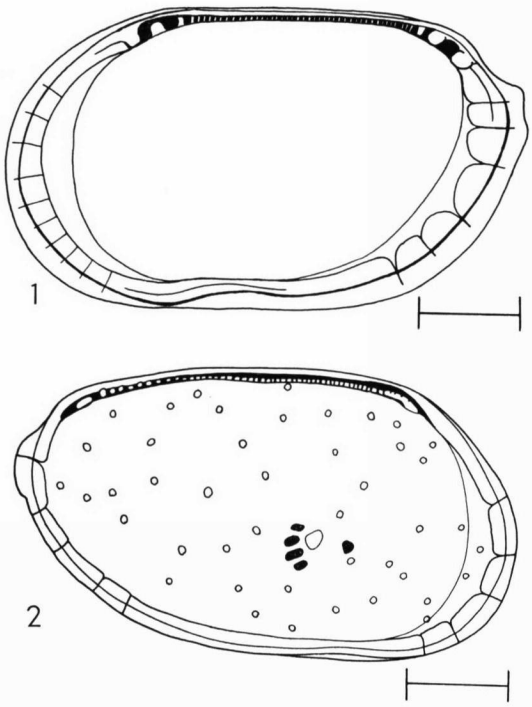


FIG. 53.—*1*. Species OE, interior of right valve.—*2*. Species OF, interior of left valve.

of closely spaced deep pits. Hinge gongylodont with crenulate median elements; radial pore canals long and straight, no vestibules present. Carapace of living specimen transparent, body and eyes purple, appendages pale yellow, genitalia darker yellow.

Type.—Adult male collected living from sta. 326 (Fig. 52,*2*). LV L, 0.56 mm.; H, 0.32 mm.; W, 0.15 mm.; RV L, 0.56 mm.; H, 0.31 mm.; W, 0.16 mm.

Habitat.—Exceedingly numerous in washings of alga BR from rocks at midtide level at Ampasimena; abundant in washings of alga-encrusted exposed mangrove pneumatophores and adjacent mud at loc. 16; *Padina*, alga type X at the Centre; other algal types; also reported from carbonate sands at the Centre, locs. 9 and 17.

Subfossil distribution.—Common in carbonate and quartzose sands from intertidal, reef, and fore-reef localities; also present in many samples of carbonate and quartz-carbonate sands and sandy clays from deeper water localities. Usually associated with sp. OB.

Species OE

Carapace small, very strongly reticulate, lacking any posterodorsal elevation or ventrolateral ridge; domicilium greatly expanded medially, greatest thickness located somewhat behind midlength and near venter, posterior margin somewhat angulate but not caudate. Hinge gongylodont with denticulate median elements, marginal area with anterior and posterior vestibules and sparse straight radial pore canals.

Type.—Intact carapace collected subfossil at sta. 473 (Fig. 53,*1*). LV L, 0.50 mm.; H, 0.30 mm.; W, 0.22 mm.; RV L, 0.50 mm.; H, 0.30 mm.; W, 0.18 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Present but never abundant in most samples of carbonate and quartzose intertidal sands, reef and fore-reef sands, and occasional sandy clays and clays.

Species OF

Carapace ovate in lateral view, moderately inflated, very fragile; exterior ornamented with fine tracery of numerous very tiny pits, conspicuous normal pore canals. Carapace translucent white, body colorless with purple markings, appendages colorless.

Type.—Female collected living at sta. 196 (Fig. 53,*2*). LV L, 0.48 mm.; H, 0.28 mm.; W, 0.15 mm.

Habitat.—Living specimens found in washings of alga type A from low tide level at loc. 1.

Subfossil distribution.—Subfossil specimens collected at three localities: shell accumulation on the lower beach at loc. 5, beach sand at low tide level at loc. 16, soft mud at low tide level at loc. 4.

Family CYTHERURIDAE G. W. Müller, 1894

Genus PARACYTHERIDEA G. W. Müller, 1894

Species RA

Very robust alate form of *Paracytheridea* with

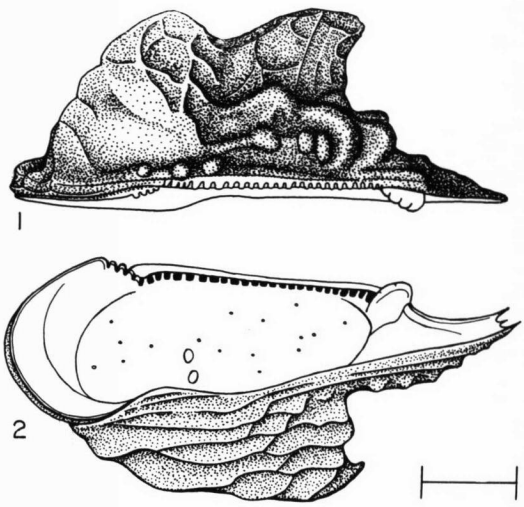


FIG. 54. Species RA.—*1*. Dorsal view of right valve.—*2*. Interior of right valve, much tilted.

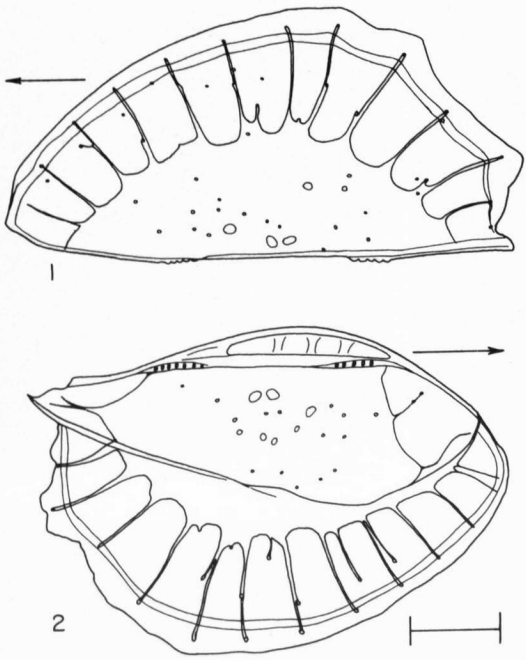


FIG. 55. Species RC.—*1*. Dorsal view of right valve.—2. Interior of left valve of different specimen, much tilted.

well developed cytheropteronid hinge. Carapace with flattened venter, broad alate swelling of domicilium, distinct median sulcus, and large posterodorsal nodes; long curved caudal process; tracery of narrow ridges on alar surfaces, irregularly gouged grooves and fossae elsewhere. Carapace of living specimen transparent white, body yellow and black, appendages yellow.

Remarks.—No adult male specimens found living in this material.

Type.—Adult female collected living at sta. 277 (Fig. 54). RV L, 0.51 mm.; H (including ala), 0.23 mm.; T, 0.22 mm.

Habitat.—Specimens recovered from washings of several kinds of algae, solitary red ascidian, and dead coral fragments at locs. 3, 6, 12, and 13, and of intertidal sand at loc. 17.

Subfossil distribution.—Subfossil specimens reported from single grab sample in carbonate sand east of Nosy Komba at 10 m.

Genus UNCERTAIN

Species RC

Carapace very small and fragile; domicilium subtriangular in cross-section with flattened venter. Frilled ventral ala extends entirely around the ventrolateral area, making outline in dorsal view nearly circular. Series of thick straight pore canals penetrate ala, ending in pores at mid-length or near edge. Hinge very delicate, in right valve consisting of crenulate anterior and posterior teeth connected by shallow groove, left valve complementary and surmounted by an arched "accommodation" groove. Subfossil carapace colorless, transparent.

Remarks.—No intact carapaces of this delicate form found.

Type.—Two subfossil specimens from sta. 401 (Fig. 55). RV L, 0.51 mm.; H (including ala), 0.30 mm.; T, 0.26 mm.; LV L, 0.56 mm.; H (including ala), 0.25 mm.; T, 0.26 mm.

Habitat.—No living specimens found.

Subfossil distribution.—Sparsely distributed in carbonate and quartz carbonate sands, muddy sands, and clays in offshore depths ranging from 2 to 24 m.

Family SCHIZOCYTHERIDAE Howe, 1961

Genus SULCOSTOCYTHERE Benson & Maddocks, 1962

Species SA

Carapace moderately large and thin-walled; anterodorsal, median, and posterior ridges developed as delicate narrow steep-walled ridges, ventrolateral ridge somewhat thicker but not alate; intervening surface areas rather irregular but only faintly reticulate. Hinge primitive three-element schizodont, consisting in right valve of anterior and posterior lobed teeth and connecting narrow locellate groove, without any anterior socket. Carapace of male longer than that of female.

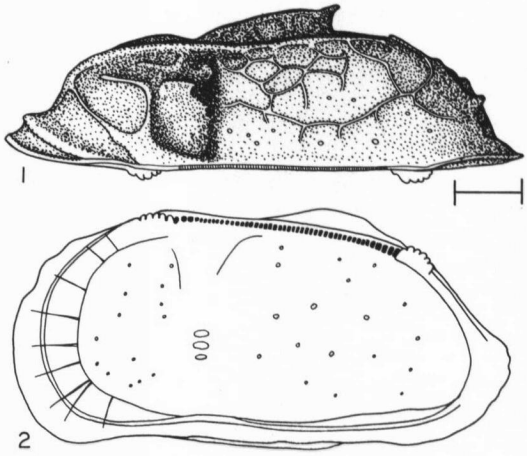


FIG. 56. Species SA.—*1*. Dorsal view of right valve.—2. Interior of right valve.

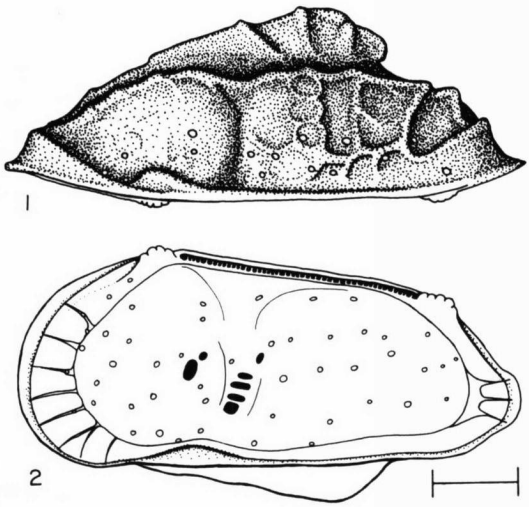


FIG. 57. Species SB.—*1*. Dorsal view of right valve.—*2*. Interior of right valve.

Carapace of living specimen transparent, body deep yellow with reddish brown patches, appendages yellow.

Type.—Adult male collected living from sta. 329B (Fig. 56). RV L, 0.74 mm.; H, 0.36 mm.

Habitat.—Intertidal mud among mangroves on the estuarine banks of locs. 4, 8, 15, and 16; intertidal quartz sand at loc. 5, 17, delta of loc. 15; occasionally found in washings of algae, dead coral fragments, and carbonate sands and sandy muds at locs. 9, 16, and Baie d'Ampasindava.

Subfossil distribution.—Common in sediments of all compositions and depths, particularly abundant in localities where found living; predominant species (to 30% of fauna) in quartz-carbonate sands and sandy muds and clays at depths of 10 to 15 m. at many stations; most abundant constituent by far of subfossil assemblages generally.

Species SB

Carapace small but robust, elongate; anterodorsal, median, and posterior ridges well developed, ventrolateral ridge developed as thick prominent ala; intermediate areas somewhat uneven but only faintly reticulate. Hinge primitive three-element schizodont, right valve consisting of anterior four-lobed tooth, narrow locellate groove, and posterior five-lobed tooth, without any anterior socket. Male carapaces more elongate than those of females. Carapace of living specimens transparent yellowish, body greenish black and yellow, appendages yellow.

Type.—Adult male collected living from sta. 467 (Fig. 57). RV L, 0.57 mm.; H, 0.25 mm.

Habitat.—Intertidal mud among mangroves on the estuarine banks of locs. 4, 8, 15, and 16; intertidal quartz sand at loc. 5; occasional specimens in washings of algae, dead coral fragments, and carbonate sand from loc. 3, 6, 7, and 10.

Subfossil distribution.—Intertidal sands and muds from locs. 4, 5, 8, and 16.

Family XESTOLEBERIDIDAE Sars, 1928

Genus XESTOLEBERIS Sars, 1866

Species XA

Carapace smooth, moderately inflated. Anterior vestibule deep, radial pore canals short and straight except in anteroventral region, where they merge proximally in groups of three. Posterior duplicature with fused portion projecting into body cavity dorsal to and constricting vestibule; radial pore canals sparse, thin, straight. Hinge strongly merodont; normal pore canals small. Carapace of living specimens transparent white to yellow, body yellow with green, brown, or reddish brown patches of varying shapes and abundance. Appendages and eggs yellow. Subfossil carapaces may retain mottled pattern of transparent and white areas.

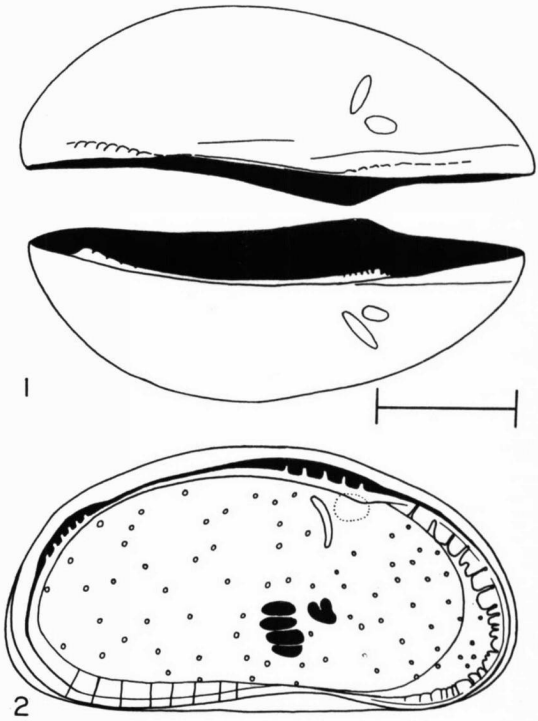


FIG. 58. Species XA.—*1*. Dorsal view of both valves.—*2*. Interior of left valve.

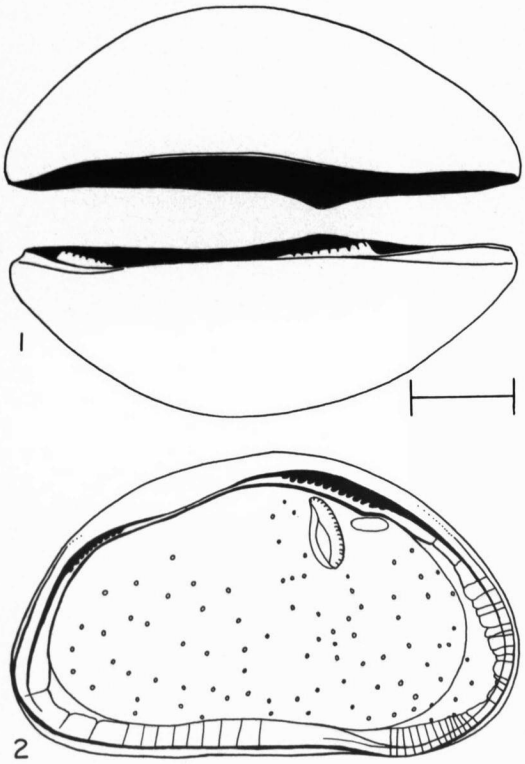


FIG. 59. Species XB.—*1*. Dorsal view of both valves.—*2*. Interior of left valve.

Remarks.—Some populations vary slightly in shape and have darker coloration than type described above, having more extensive colored patches of dark brown to red. Even more typical green forms vary considerably among populations in hue and intensity, apparently correlated to some extent with the color of the plant from which they were collected. No consistently distinguishable differences were observed that would justify separation of these variants as distinct species.

Type.—Adult male of typical yellow and greenish brown color collected living at sta. 450 (Fig. 58). LV L, 0.51 mm.; H, 0.29 mm.; RV L, 0.49 mm.; H, 0.28 mm.

Habitat.—By far the most abundant and diversified species, in numbers of specimens, numbers of stations, and types of localities collected. Nearly ubiquitous in reef environments; found in washings of algae, grasses, sponges, living corals, dead coral fragment accumulations. Also reported from carbonate reef sands at loc. 1 and 13, intertidal quartz sand at loc. 5.

Subfossil distribution.—Widely distributed but never abundant in carbonate and quartzose sands and sandy muds in intertidal, reef, and fore-reef localities and at depths of 20 to 25 m. north of loc. 12.

Species XB

Carapace of male robust, inflated, thickest slightly behind midlength and ventrally; subtrapezoidal in lateral view, with distinctly acute posteroventral angle; venter flattened. Exterior finely pitted in incipiently reticulate pattern, emphasized by conspicuous normal pore canals in rows paralleling venter. Hinge robust merodont, postocular scar thick elongate ridge. Vestibules very shallow; radial pore canals thin, straight, irregularly spaced. Carapace of living specimen subopaque white with normal pore canals distinctly visible as white dots. Body and appendages light greenish yellow.

Type.—Adult male collected living from sta. 527 (Fig. 59). LV L, 0.49 mm.; H, 0.29 mm.; RV L, 0.48 mm.; H, 0.28 mm.

Habitat.—Common and occasionally quite abundant in washings of algae of many types, dead coral fragments, sponges, grasses, and associated sand.

Subfossil distribution.—Widely distributed but never abundant in intertidal, reef, and fore-reef carbonate sands at many localities.

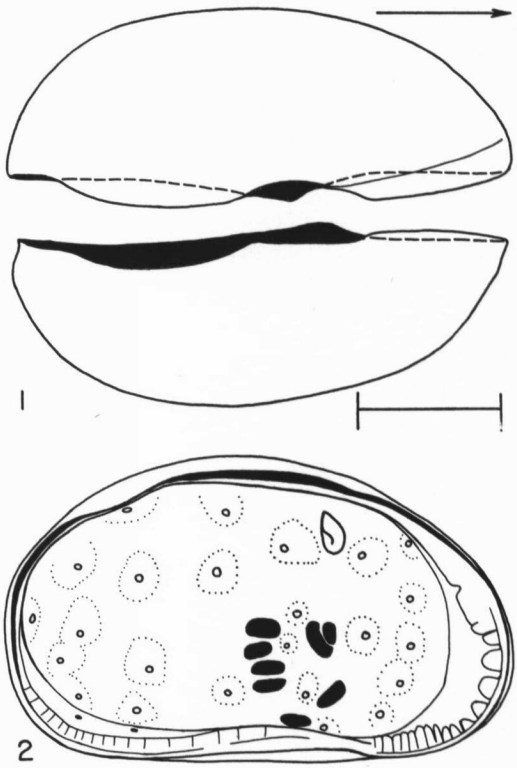


FIG. 60. Species XC.—*1*. Dorsal view of both valves.—*2*. Interior of left valve, showing white opaque areas around normal pore canals.

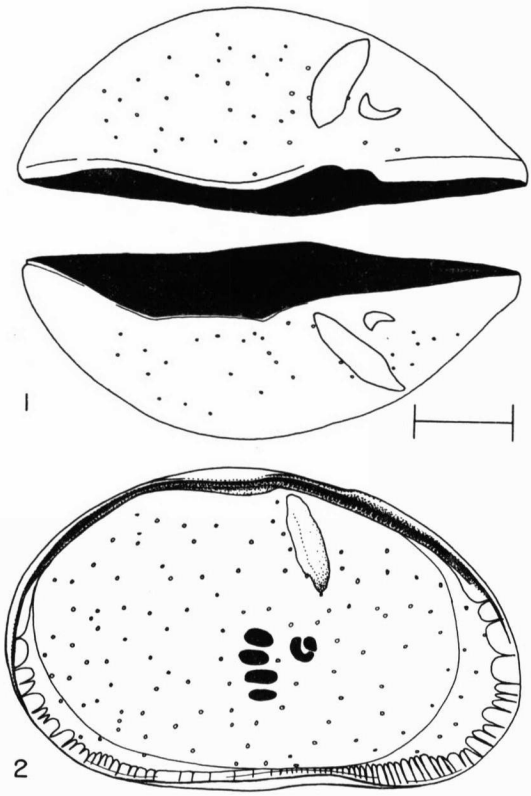


FIG. 61. Species XE.—*1*. Dorsal view of both valves.—*2*. Interior of left valve.

Species XC

Carapace very small and robust, inflated, smooth, venter flattened, posterior bluntly truncated. Normal pore canals very few in number but extremely large and conspicuous. Vestibules shallow, five anterior pore canals short and thick, others thin, none branching. Appearance of living specimen pale pink with large white dots corresponding to opaque areas around normal pore canals. Subfossil carapace translucent white with opaque white spots.

Type.—Adult male collected living at sta. 476 (Fig. 60). LV L, 0.34 mm.; H, 0.21 mm.; RV L, 0.33 mm.; H, 0.30 mm.

Habitat.—Common and quite numerous in reef sands among coral masses.

Subfossil distribution.—Subfossil specimens found in carbonate sand among corals at loc. 1, south of loc. 1 at 10 m. depth, and muddy sand south of Hellville at 20 m.

Species XE

Carapace smooth, globose, thickest slightly behind midlength; anterior and posterior margins broadly rounded, dorsal margin highly arched; with minimal sexual dimorphism. Postocular scar an elongate triangular ridge. Radial pore canals simple, widening proximally, irregularly spaced around free margin, especially close in anteroventral region. Carapace of living specimen colorless transparent, glassy, body yellow-brown.

Type.—Adult male collected living from sta. 080 (Fig. 61). LV L, 0.52 mm.; H, 0.33 mm.; RV L, 0.50 mm.; H, 0.31 mm.

Habitat.—Common in washings of several kinds of algae, *Thallassia*, associated intertidal and reef sands, dead coral fragments.

Subfossil distribution.—Common but rarely abundant in intertidal, reef, and fore-reef sands, also in carbonate and quartz-carbonate sands and muddy sands at 10 to 15 m. in various localities.

Species XF

Carapace rather elongate, inflated, smooth. Hinge robust merodont; duplicature shallow, without posterior vestibule, radial pore canals simple; postocular scar long and arcuate; normal pore canals small, numerous. Carapace of living specimen translucent white with normal pore canals conspicuous as tiny white dots, surface ir-

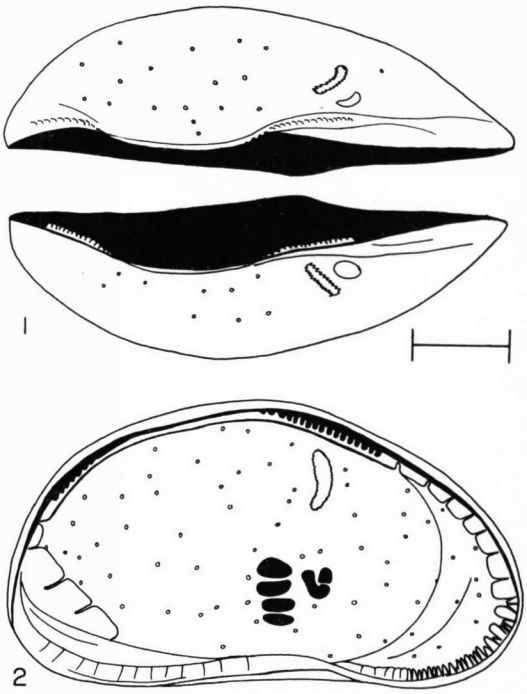


FIG. 62. Species XF.—*1*. Dorsal view of both valves.—*2*. Interior of left valve.

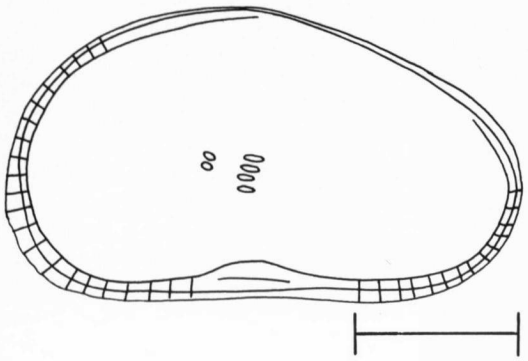


FIG. 63. Species JC, interior of right valve.

ridescent with predominantly yellow cast. Body pale green, eyes red, eggs yellow.

Type.—Adult male collected living from sta. 220 (Fig. 62). LV L, 0.36 mm.; H, 0.18 mm.; RV L, 0.35 mm.; H, 0.17 mm.

Habitat.—Very abundant in one collection of dead coral fragments at loc. 12; also found there on an alcyonarian and on dead coral fragments at loc. 9.

Family UNCERTAIN

Genus UNCERTAIN

Species JC

Remarks.—Specimens of this category are juveniles, most probably of sp. NA, family Cytherideidae. Exterior of carapace very finely pitted. Both carapace and body are yellow in color.

Type.—Juvenile collected living from sta. 252 (Fig. 63). RV L, 0.33 mm.; H, 0.19 mm.

Habitat.—Collected from alga type X at the Centre, intertidal mud among mangrove roots at loc. 16.

Subfossil distribution.—No subfossil specimens assigned to this category.

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